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A Method of Fitting Growth Curves of the von Bertalanffy Type to Observed Data[1]

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ABSTRACT

A method is described for obtaining the best least-squares estimates of the parameters L_∞, k, and t_0 when von Bertalanffy curves of the type

$$L = L_\infty (1 - e^{-k(t-t_0)})$$

are fitted to observed data. This method imposes no restrictions on the number or size of the samples or on the time intervals between them. It also provides estimates of the limits of error of the parameters. The amount of computation is fairly large, but a method of systematizing it is described which makes manual computation practicable for moderate-sized sets of data. The method has been used to develop a computer program which seems to have advantages over some existing methods.

A numerical example is worked out in full to illustrate application of the method.

INTRODUCTION

Mathematical models based on the concept that the rate of growth of an animal is related to the amount by which its size falls short of an ultimate maximum have been widely used in fisheries research, particularly following their application to the general theory of fishing by Beverton and Holt (1957). This concept, which was developed by von Bertalanffy as part of the general application of open system theory to biological systems, can be expressed in a variety of mathematical forms, but those proposed by Beverton and Holt are generally appropriate in fisheries work. These are:

$$l_t = L_\infty(1 - e^{-k(t-t_0)}) \quad \ldots \quad \ldots \qquad (1)$$

and

$$w_t = W_\infty(1 - e^{-k(t-t_0)})^3 \quad \ldots \quad \ldots \qquad (2)$$

where l_t and w_t are the length and weight at age t, L_∞ and W_∞ are the theoretical maximum length and weight, and k and t_0 are constants, the latter being the age at which growth following this law theoretically commences.

Fitting either of these curves to observed data involves determining values for k and t_0, and either L_∞ or W_∞ as appropriate. The basic data generally consist of a number of observations of the size and age of individual animals. A variety of methods of fitting a curve of the above type to such data have

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been employed. But some of these only yield very approximate results as has been pointed out by Stevens (1951), who has reviewed the general question extensively. Stevens has himself developed a maximum likelihood method of fitting curves of the type

$$y = \alpha + \beta\rho^x \quad .. \quad .. \quad .. \quad .. \quad (3)$$

of which the Beverton and Holt equations are of course special cases. His method is efficient, and involves relatively little computation provided that the data consist of not more than seven observations at equally spaced intervals of time and that equal weight can be given to each such observation. The method may be applied to a greater number of observations or to unevenly spaced observations, but in these cases the amount of computation is greatly increased since the tables provided are not applicable. The method also provides an estimate of the standard error of ρ and hence would provide one for k in the Beverton and Holt equations.

More recently, Tomlinson and Abramson (1961) have described a procedure for obtaining a least-squares estimate by using a procedure essentially based on that of Stevens. Abramson (1965) has described a computer program based on this method. Like that of Stevens, the method requires the samples to be at equal intervals of time; provided that there are not more than 18 samples and that they are also of equal size, tables provided by Tomlinson and Abramson can be used, and the method is a rapid one. It is applicable in principle to samples of unequal size but in this case the amount of computation would be very substantial.

Beverton and Holt (1957) have also reviewed the problem and have proposed a graphical method of determining the various constants. This could be relatively rapid but will only yield approximate results, particularly for W_∞ and t_0. It also requires observations at equal intervals of time and gives equal weight to the data for each time.

The present paper also proposes a least-squares method of estimating the various constants, but one which has no limitation on the spacing of the observations and gives equal weight to all individual observations. It also avoids the loss of efficiency which occurs in Stevens' method in converting the data for each time interval into a single mean value. The amount of computation involved is substantially greater than that required by the methods of Stevens and Tomlinson and Abramson within the limits of their tables, but it is not excessive with proper organization as outlined in this paper. The method seems particularly suitable for cases where it is desired to make the maximum use of a relatively small amount of data, and where the ages are irregularly spaced but precisely known. It can also be used to obtain estimates of k and L_∞ where t_0 is arbitrarily fixed for biological or other reasons, including the case where $t_0 = 0$.

Before applying any of the more elaborate methods for fitting a von Bertalanffy curve to actual data, it is sometimes necessary to make an arbitrary decision as to the age range over which a fit is to be attempted. In particular, it may be desirable to discard some of the earliest points either because of apparent differences in the nature of the growth curve at this stage, or because of doubts as to whether these observations have been subject to some selection. Graphical methods such as those of Beverton and Holt probably provide the best basis for deciding which points, if any, should be discarded. Any discarding of data because they are likely to reduce the goodness of fit to the desired type of curve will, however, adversely affect the meaning of any estimates of the probable errors of estimate of the various parameters; while the methods still describe the goodness of fit to the data actually fitted, the fit to the total original data has been affected by the arbitrary decision as to what part of them is to be fitted. Different decisions in this respect would produce different estimates of the probable errors.

DERIVATION

An equation of the type of equation 1 is considered first. This may be written:

$$l = L_\infty - L_\infty e^{kt_0} e^{-kt} \tag{3}$$

which gives a linear regression of l upon e^{-kt} of the type

$$l = a + b\, e^{-kt},$$

where $a = L_\infty$

and $b = -L_\infty e^{kt_0}$.

Applying standard methods of regression analysis we obtain

$$\hat{a} = \frac{\Sigma l}{N - e^{kt_0}\Sigma e^{-kt}} \tag{4}$$

and

$$\hat{b} = \frac{N\Sigma l e^{-kt} - \Sigma l \Sigma e^{-kt}}{N\Sigma e^{-2kt} - (\Sigma e^{-kt})^2} \tag{5}$$

where N is the number of observations.

Eliminating L_∞ gives an equation in k and t_0

$$\frac{\Sigma l}{N - e^{kt_0}\Sigma e^{-kt}} = \frac{N\Sigma l e^{-kt} - \Sigma l \Sigma e^{-kt}}{e^{kt_0}[(\Sigma e^{-kt})^2 - N\Sigma e^{-2kt}]} \tag{6}$$

which simplifies to

$$N\Sigma l e^{-kt} - \Sigma l \Sigma e^{-kt} - e^{kt_0}\Sigma e^{-kt}\Sigma l e^{-kt} + e^{kt_0}\Sigma l \Sigma e^{-2kt} = 0 \tag{7}$$

As will be discussed later this can be solved for either k or t_0 when the other quantity is known and will provide the best least-squares fit under the given conditions.

If, however, none of the three parameters involved is known initially a further approach is required and the following method may be used.

If a value of k is chosen arbitrarily, and a regression line is fitted by the above procedure, the sum of the squares of the deviations from regression is given by

$$\Sigma l^2 - \frac{(\Sigma l)^2}{\mathrm{N}} - \frac{(\mathrm{N}\Sigma l e^{-kt} - \Sigma l \Sigma e^{-kt})^2}{\mathrm{N}[\mathrm{N}\Sigma e^{-2kt} - (\Sigma e^{-kt})^2]}.$$

The magnitude of this sum of squares is independent of L_∞ and t_0, but will vary with the value of k. The best fit, by the least-squares criterion, will therefore be that for which this expression is a minimum. Since the first two terms do not include k, this involves maximizing the third term.

The desired value of k is therefore that which fulfils the condition

$$\mathrm{D}_k\left[\frac{(\mathrm{N}\Sigma l e^{-kt} - \Sigma l \Sigma e^{-kt})^2}{\mathrm{N}[\mathrm{N}\Sigma e^{-2kt} - (\Sigma e^{-kt})^2]}\right] = 0 \quad .. \quad .. \quad .. \quad (8)$$

Differentiating and multiplying by the constant N, we obtain after a little simplification

$$\underline{[\mathrm{N}\Sigma e^{-2kt} - (\Sigma e^{-kt})^2]\ [\mathrm{N}\Sigma l e^{-kt} - \Sigma l \Sigma e^{-kt}]\ [\Sigma l \Sigma t e^{-kt} - \mathrm{N}\Sigma l t e^{-kt}] -}$$

$$\frac{(\mathrm{N}\Sigma l e^{-kt} - \Sigma l \Sigma e^{-kt})^2\ (\Sigma e^{-kt}\Sigma t e^{-kt} - \mathrm{N}\Sigma e^{-2kt})}{[\mathrm{N}\Sigma e^{-2kt} - (\Sigma e^{-kt})^2]^2} = 0 \quad .. \quad (9)$$

Unless the points all lie precisely on the regression line, and in this case the method is unnecessary, the quantities $(\mathrm{N}\Sigma l e^{-kt} - \Sigma l \Sigma e^{-kt})$ and $(\mathrm{N}\Sigma e^{-2kt} - (\Sigma e^{-kt})^2)$ will not equal zero and they may therefore be divided out, reducing the equation to

$$[\mathrm{N}\Sigma e^{-2kt} - (\Sigma e^{-kt})^2]\ [\Sigma l \Sigma t e^{-kt} - \mathrm{N}\Sigma l t e^{-kt}] -$$

$$(\mathrm{N}\Sigma l e^{-kt} - \Sigma l \Sigma e^{-kt})\ (\Sigma e^{-kt}\Sigma t e^{-kt} - \mathrm{N}\Sigma t e^{-2kt}) = 0 \quad .. \quad (10)$$

This equation may be solved for k by Newton's method; the procedure is iterative, but, provided the initial trial value is well chosen, very few steps are necessary to obtain sufficient accuracy for most purposes.

If the expression on the left hand side of equation 10 is called α, we may differentiate with respect to k to get

$$\begin{aligned} \mathrm{D}_k(\alpha) = {} & [\mathrm{N}\Sigma \mathrm{e}^{-2kt} - (\Sigma \mathrm{e}^{-kt})^2]\ [\mathrm{N}\Sigma l t^2 \mathrm{e}^{-kt} - \Sigma l \Sigma t^2 \mathrm{e}^{-kt}] + \\ & (\Sigma \mathrm{e}^{-kt}\Sigma t \mathrm{e}^{-kt} - \mathrm{N}\Sigma t \mathrm{e}^{-2kt})\ (\Sigma l \Sigma t \mathrm{e}^{-kt} - \mathrm{N}\Sigma l t \mathrm{e}^{-kt}) - \\ & [\mathrm{N}\Sigma l \mathrm{e}^{-kt} - \Sigma l \Sigma \mathrm{e}^{-kt}]\ [2\mathrm{N}\Sigma t^2 \mathrm{e}^{-2kt} - (\Sigma t \mathrm{e}^{-kt})^2 - \Sigma \mathrm{e}^{-kt}\Sigma t^2 \mathrm{e}^{-kt}] \quad \cdot\cdot \quad \cdot\cdot \quad (11) \end{aligned}$$

If the arbitrarily chosen first approximation to k is called k_1, and this value is inserted in equations 10 and 11, we obtain values for α and $\mathrm{D}_k(\alpha)$ which may be called α_1 and $\mathrm{D}_k(\alpha)_1$. The estimated error in k is then $-\dfrac{\alpha_1}{\mathrm{D}_k(\alpha)_1}$ so that the first corrected estimate of $k = k_1 - \dfrac{\alpha_1}{\mathrm{D}_k(\alpha)_1} = k_2$. A second and greatly improved estimate of k is then obtained as $k_3 = k_2 - \dfrac{\alpha_2}{\mathrm{D}_k(\alpha)_2}$ where α_2 and $\mathrm{D}_k(\alpha)_2$ are values obtained by inserting k_2 in 10 and 11. If necessary, further corrections can be made, until their small size indicates that the desired level of accuracy has been reached. As the proportional change in $\mathrm{D}_k(\alpha)$ with k is small compared with that of α it may be unnecessary to compute further values for $\mathrm{D}_k(\alpha)$, but to use $\mathrm{D}_k(\alpha)_2$ as the denominator for all higher order corrections.

When k has been determined with the desired level of accuracy by this method, equation 7 can be used to determine t_0. For this purpose it can be written

$$\mathrm{e}^{kt_0} = -\frac{\mathrm{N}\Sigma l \mathrm{e}^{-kt} - \Sigma l \Sigma \mathrm{e}^{-kt}}{\Sigma l \Sigma \mathrm{e}^{-2kt} - \Sigma \mathrm{e}^{-kt}\Sigma l \mathrm{e}^{-kt}} \quad \cdot\cdot \quad \cdot\cdot \quad \cdot\cdot \quad (12)$$

so that

$$t_0 = \frac{\log_e (\Sigma l \Sigma \mathrm{e}^{-kt} - \mathrm{N}\Sigma l \mathrm{e}^{-kt}) - \log_e (\Sigma l \Sigma \mathrm{e}^{-2kt} - \Sigma \mathrm{e}^{-kt}\Sigma l \mathrm{e}^{-kt})}{k} \quad \cdot\cdot \quad (13)$$

A practical difficulty arises in that k has been determined to one higher degree of accuracy than has been used to determine the expression in the numerator of this equation, and since the value of the numerator varies rather fast in relation to k an appreciable error is introduced by using the values based on the preceding estimate of k. This can of course be overcome by recalculating the values for the final estimate of k, but this is laborious. It can, however, be avoided since, approximately,

$$\begin{aligned} & [\log_e (\Sigma l \Sigma \mathrm{e}^{-kt} - \mathrm{N}\Sigma l \mathrm{e}^{-kt}) - \log_e (\Sigma l \Sigma \mathrm{e}^{-2kt} - \Sigma \mathrm{e}^{-kt}\Sigma l \mathrm{e}^{-kt})]_{k+\delta k} \\ & = [\log_e (\Sigma l \Sigma \mathrm{e}^{-kt} - \mathrm{N}\Sigma l \mathrm{e}^{-kt}) - \log_e (\Sigma l \Sigma \mathrm{e}^{-2kt} - \Sigma \mathrm{e}^{-kt}\Sigma l \mathrm{e}^{-kt})]_k \\ & + \delta k \mathrm{D}_k[\log_e (\Sigma l \Sigma \mathrm{e}^{-kt} - \mathrm{N}\Sigma l \mathrm{e}^{-kt}) - \log_e (\Sigma l \Sigma \mathrm{e}^{-2kt} - \Sigma e^{-kt}\Sigma l \mathrm{e}^{-kt})]_k \quad \cdot\cdot \quad \cdot\cdot \quad (14) \end{aligned}$$

where the subscripts k and $k + \delta k$ indicate the values when k is equal to k and $k + \delta k$, respectively, and δk is a small increase in k.

Differentiation gives

$$D_k[\log_e(\Sigma l\Sigma e^{-kt} - N\Sigma le^{-kt}) - \log_e(\Sigma l\Sigma e^{-2kt} - \Sigma e^{-kt}\Sigma le^{-kt})]$$

$$= \frac{(\Sigma l\Sigma e^{-2kt} - \Sigma e^{-kt}\Sigma le^{-kt})(N\Sigma lte^{-kt} - \Sigma l\Sigma te^{-kt}) - (\Sigma l\Sigma e^{-kt} - N\Sigma le^{-kt})(\Sigma e^{-kt}\Sigma lte^{-kt} + \Sigma le^{-kt}\Sigma te^{-kt} - 2\Sigma l\Sigma te^{-2kt})}{(\Sigma l\Sigma e^{-kt} - N\Sigma le^{-kt})(\Sigma l\Sigma e^{-2kt} - \Sigma e^{-kt}\Sigma le^{-kt})} \quad .. \quad (15)$$

This expression can be evaluated for the penultimate value of *k*, and by substituting in equation 14, and using δk for the final adjustment of *k*, a good estimate of the correct value of the numerator in equation 13, and hence of t_0, is obtained.

L_∞ can now be determined from equations 4 and 5. Combining either of these with equation 12 gives, when simplified

$$L_\infty = \frac{\Sigma l\Sigma e^{-2kt} - \Sigma e^{-kt}\Sigma le^{-kt}}{N\Sigma e^{-2kt} - (\Sigma e^{-kt})^2} \quad .. \quad .. \quad .. \quad (16)$$

The value of L_∞ can thus be calculated directly for the highest order approximation for *k* for which the various sums of functions of e^{-kt} have been determined. To determine the value for the final estimate of *k* the same procedure can be followed as for t_0. Differentiating 16 gives

$$D_k(L_\infty) = \frac{[N\Sigma e^{-2kt} - (\Sigma e^{-kt})^2][\Sigma e^{-kt}\Sigma lte^{-kt} + \Sigma te^{-kt}\Sigma le^{-kt} - 2\Sigma l\Sigma te^{-2kt}] - 2[\Sigma l\Sigma e^{-2kt} - \Sigma e^{-kt}\Sigma le^{-kt}][\Sigma e^{-kt}\Sigma te^{-kt} - N\Sigma te^{-2kt}]}{[N\Sigma e^{-2kt} - (\Sigma e^{-kt})^2]^2} \quad .. \quad (17)$$

Evaluating this and multiplying by the final adjustment of *k* will give the final correction to be made to the estimate of L_∞.

DETERMINATION OF *k* WHEN t_0 IS KNOWN

If for any reason it is desirable to adopt a value of t_0 which has been determined by other considerations, equation 7 can be used to determine the value of *k* which will provide the best fit to the data. Again Newton's method may be used. Calling the expression on the left-hand side of equation 7 β, and differentiating, we get, with some simplification,

$$D_k(\beta) = -(N\Sigma lte^{-kt} - \Sigma l\Sigma te^{-kt}) + e^{kt_0}(\Sigma le^{-kt}\Sigma te^{-kt} + \Sigma e^{-kt}\Sigma lte^{-kt} - 2\Sigma l\Sigma te^{-2kt}) + t_0e^{kt_0}(\Sigma l\Sigma e^{-2kt} - \Sigma e^{-kt}\Sigma le^{-kt}) \quad .. \quad (18)$$

Taking k_1 as a first approximation to *k* and inserting in 7 and 18 to obtain β_1, and $D_k(\beta)_1$, gives an estimate of $k = k_2 = k_1 - \frac{\beta_1}{D_k(\beta)_1}$.

The estimate can again be improved to any desired level of accuracy by inserting the corrected values in the equations for β and $D_k(\beta)$ as often as desired.

When k has been determined in this way, L_∞ can again be determined by using equation 16.

Taking $t_0 = 0$ is of course a special case of this situation. Since $t_0 e^{kt_0} = 0$ and $e^{kt_0} = 1$, equations 7 and 18 are simplified and become
Equation 7:

$$-N\Sigma l e^{-kt} - \Sigma l \Sigma e^{-kt} - \Sigma e^{-kt} \Sigma l e^{-kt} + \Sigma l \Sigma e^{-2kt} = \beta = 0 \quad .. \quad .. \quad (19)$$

Equation 18:

$$D_k(\beta) = -(N\Sigma l t e^{-kt} - \Sigma l \Sigma t e^{-kt}) + (\Sigma l e^{-kt} \Sigma t e^{-kt} + \Sigma e^{-kt} \Sigma l t e^{-kt} - 2\Sigma l \Sigma t e^{-2kt}) \quad .. \quad (20)$$

Solution for k then proceeds as before.

APPLICATION TO THE WEIGHT EQUATION

The foregoing discussion has dealt with growth in length as described by equation 1. For growth in weight, equation 2 is applicable if growth is isometric, and in this case the same method of fitting may be employed by transforming the equation to

$$W^{1/3} = W_\infty^{1/3} [1 - e^{-k(t-t_0)}].$$

The original weight data are therefore transformed to their cube roots and the identical procedure followed. The constants k and t_0 have the same biological significance as those obtained by fitting length data. Application of equation 16 will, however, give estimates of $W_\infty^{1/3}$, which must be cubed to give estimates of W_∞.

In many fishes, however, growth is allometric and the length–weight relationship can be satisfactorily described by

$$W = Pl^\gamma$$

where γ has a value other than 3. In such instances, the same method may be employed by using the equation

$$W_\infty^{\frac{1}{\gamma}} = W^{\frac{1}{\gamma}} [1 - e^{-k(t-t_0)}]$$

and raising the resulting estimates of $W^{\frac{1}{\gamma}}$ to the power of γ to obtain estimates of W.

In using the von Bertalanffy equation to compute yield isopleths by the methods of Beverton and Holt (1957) it is necessary to take the exponent of the length–weight relation to be 3 unless the technique of Paulik and Gales (1964) is employed. Paulik and Gales have, however, pointed out that provided adequate weight–age data are available it is better to fit the von Bertalanffy curve to the cube root of the weight than to the length even when the exponent is not 3.

COMPUTATION PROCEDURE

Though the computations outlined above appear substantial they are somewhat simplified by the fact that some of the expressions involved occur in more than one equation, and can therefore, when once determined, be easily inserted wherever required.

To simplify calculation the various quantities can be denoted by symbols as, for example, in the following scheme.

The primary quantities required are:

$A = N$

$B = \Sigma l$

$C = \Sigma e^{-kt}$

$D = \Sigma l e^{-kt}$

$E = \Sigma e^{-2kt}$

$F = \Sigma l t e^{-kt}$

$G = \Sigma t e^{-kt}$

$H = \Sigma t e^{-2kt}$

$I = \Sigma t^2 e^{-2kt}$

$J = \Sigma t^2 e^{-kt}$

$L = \Sigma l t^2 e^{-kt}$

From these the following secondary expressions are derived:

$M = BE - CD$

$P = AD - BC$

$Q = AE - C^2$

$R = \frac{1}{2} D_k(Q) = CG - AH$

$S = D_k(P) = BG - AF$

$T = D_k(R) = 2AI - G^2 - CJ$

$U = D_k(S) = AL - BJ$

$V = D_k(M) = GD + CF - 2BH$

The main equations required in the calculations can now be rewritten thus:

Equation 7: $P + Me^{kt_0} = \beta = 0$ .. .. (7A)

Equation 10: $QS - PR = \alpha = 0$ .. .. (10A)

Equation 11: $QU + RS - PT = D_k(\alpha)$ .. .. (11A)

Equation 12: $e^{kt_0} = -\frac{P}{M}$ .. .. (12A)

Equation 13: $t_0 = \frac{\log_e(-P) - \log_e(M)}{k}$ .. .. (13A)

Equation 14: $(\log_e(-P) - \log_e(M))_{k+\delta k} = (\log_e(-P) - \log_e(M))_k + \delta k D_k(\log_e(-P) - \log_e(M))_k$ .. (14A)

Equation 15: $D_k(\log_e(-P) - \log_e(M)) = \dfrac{SM - PV}{PM}$ .. .. .. (15A)

Equation 16: $L_\infty = \dfrac{M}{Q}$ .. .. (16A)

Equation 17: $D_k(L_\infty) = \dfrac{QV - 2MR}{Q^2}$ .. .. (17A)

Equation 18: $D_k(\beta) = S + Ve^{kt_0} + Mt_0e^{kt_0}$ .. .. (18A)

Equation 19: $P + M = \beta = 0$ .. .. (19A)

Equation 20: $D_k(\beta) = S + V$ .. .. (20A)

If t_0 is known or assumed and the procedure described in the preceding section is being followed it is not necessary to determine the quantities I, J, L, T, and U.

An important factor in the calculations is the selection of an appropriate first approximation to k, since the closer this is to the true value the fewer steps will be required to obtain any desired level of accuracy. A great many ways of making the selection are possible, ranging from intuition or previous experience to some simpler analysis of the same data. Some of these have been reviewed by Stevens, who advocates drawing a freehand curve through the points and then basing the estimate on three convenient points on it. This has the advantage of not requiring a visual estimate of the asymptotic level. Where, however, it is reasonably possible to make rough estimates of L_∞ and t_0 a very simple method may give a sufficiently accurate result. This is to determine from the curve the time ($t_{.5}$) at which the length reaches 50% of the asymptotic value and then estimate k from the formula

$$k = \frac{\log_e 0.5}{t_{.5} - t_0} = \frac{.6931}{t_{.5} - t_0}.$$

It should be noted that the value of k obtained in this way is very sensitive to the value selected for t_0.

The systematized method of computation described above has provided a basis for a computer program for fitting curves of this type. This program, to be described shortly elsewhere, does not have the limitations regarding equality of time intervals required by the program of Abramson (1965). Also, Turnbull (in Southward and Chapman, 1965) has developed a program for fitting a more general class of growth equations, which would include the form dealt with here as a special case.

ERRORS OF ESTIMATES

The errors of estimate of the parameters to be determined cannot easily be obtained directly from the method outlined above. Once the parameters have been estimated, however, it is possible to apply a technique based on the method outlined by Gomes (1953) following Stevens (1951).

The normal equations on which the least-squares solution is based can be written in the form

$$\left.\begin{aligned}
&NL_\infty + L_\infty e^{2kt_0}\Sigma e^{-2kt} - \Sigma l + e^{kt_0}\Sigma l e^{-kt} - 2L_\infty e^{kt_0}\Sigma e^{-kt} = 0\\
&L_\infty^2 k e^{2kt_0}\Sigma e^{-2kt} + L_\infty k e^{kt_0}\Sigma l e^{-kt} - L_\infty^2 k e^{kt_0}\Sigma e^{-kt} = 0\\
&L_\infty^2 t_0 e^{2kt_0}\Sigma e^{-2kt} - L_\infty^2 e^{2kt_0}\Sigma t e^{-2kt} + L_\infty t_0 e^{kt_0}\Sigma l e^{-kt} - L_\infty e^{kt_0}\Sigma l t e^{-kt} -\\
&\qquad L_\infty t_0 e^{kt_0}\Sigma e^{-kt} + L_\infty e^{kt_0}\Sigma t e^{-kt} = 0
\end{aligned}\right\} \quad \ldots \quad \ldots \quad (22)$$

From these equations the information matrix can be obtained by following the same method as Stevens and differentiating in turn in respect to L_∞, t_0, and k and putting l equal to its expected value. The resulting matrix may be written

$$\left|\,\mathrm{In}\,\right| = \left|\begin{matrix} a_1 b_1 c_1 \\ a_2 b_2 c_2 \\ a_3 b_3 c_3 \end{matrix}\right|$$

where

$$\left.\begin{aligned}
a_1 &= N + e^{2kt_0}\Sigma e^{-2kt} - 2e^{kt_0}\Sigma e^{-kt}\\
a_2 &= L_\infty k e^{kt_0}[e^{kt_0}\Sigma e^{-2kt} - \Sigma e^{-kt}]\\
a_3 &= L_\infty e^{kt_0}[t_0 e^{kt_0}\Sigma e^{-2kt} - e^{kt_0}\Sigma t e^{-kt} - t_0\Sigma e^{-kt} + \Sigma t e^{-kt}]\\
b_1 &= a_2\\
b_2 &= L_\infty^2 k^2 e^{2kt_0}\Sigma e^{-2kt}\\
b_3 &= L_\infty^2 k e^{2kt_0}[t_0\Sigma e^{-2kt} - \Sigma t e^{-2kt}]\\
c_1 &= a_3\\
c_2 &= b_3\\
c_3 &= L_\infty^2 e^{2kt_0}[t_0^2\Sigma e^{-2kt} - 2t_0\Sigma t e^{-2kt} + \Sigma t^2 e^{-2kt}]
\end{aligned}\right\} \quad \ldots \quad \ldots \quad (23)$$

Rewriting, using the previous symbols for the various sums and putting $Z = e^{kt_0}$, we get

$$\left.\begin{aligned}
a_1 &= A + Z^2E - 2ZC \\
a_2 &= L_\infty kZ(ZE - C) = b_1 = p \\
a_3 &= L_\infty Z^2(t_0E - H) + LZ(G - t_0C) = c_1 = r \\
b_2 &= L_\infty^2 k^2 Z^2 E \\
b_3 &= L_\infty^2 kZ^2(t_0E - H) = c_2 = q \\
c_3 &= L_\infty^2 Z^2[t_0^2E - 2t_0H + I]
\end{aligned}\right\} \quad \cdots \quad \cdots \quad (24)$$

Inverting this matrix gives the correlation matrix

$$\begin{vmatrix} \text{Cor} \end{vmatrix} = \begin{vmatrix} a_1' & b_1' & c_1' \\ a_2' & b_2' & c_2' \\ a_3' & b_3' & c_3' \end{vmatrix}$$

Following Stevens, estimates of the variances of the parameters in the original equation, L_∞, t_0, and k, are given, respectively, by

$$\hat{V}(L_\infty) = a_1's^2 \quad \cdots \quad (25)$$

$$\hat{V}(t_0) = b_2's^2 \quad \cdots \quad (26)$$

$$\hat{V}(k) = c_3's^2 \quad \cdots \quad (27)$$

where s^2 is the mean square of the residual deviations, and can be obtained by dividing the expression for the sum of the squares of the deviations from regression given on p. 166 by the degrees of freedom. Converting to the standardized symbols for the sums and their deviations, this leads to

$$s^2 = \frac{\Sigma l^2 - \dfrac{B^2}{A} - \dfrac{P^2}{AQ}}{A - 3} \quad \cdots \quad \cdots \quad \cdots \quad (28)$$

By evaluating the correlation matrix we can write the estimates of the variances as

$$\left.\begin{aligned} \hat{V}(L_\infty) &= \frac{b_2c_3 - q^2}{\Delta}\cdot s^2 \\ \hat{V}(t_0) &= \frac{c_3a_1 - r^2}{\Delta}\cdot s^2 \\ \hat{V}(k) &= \frac{a_1b_2 - p^2}{\Delta}\cdot s^2 \end{aligned}\right\} \quad \ldots \quad \ldots \quad (29)$$

where

$$\Delta = a_1b_2c_3 + 2pqr - a_1q^2 - b_2r^2 - c_3p^2 \quad \ldots \quad \ldots \quad (30)$$

The variances can therefore be relatively easily calculated when the terms of the information matrix have been computed. The standard errors are then determined as the square roots of the variances.

As pointed out by Stevens it is not strictly correct to use Student's *t* to determine fiducial limits here, but it probably still provides the best approximation available.

EXAMPLE

The procedure may be illustrated with the following hypothetical example representing the lengths of eight fish of known ages.

Age (*t*)	1	2	2	3	4	5	5	7
Length (*l*)	2	3	4	5	5	5	6	6

A rough preliminary estimate of *k* by the method described above gives a value $k_1 = 0.3$.

Using this value the following are obtained for the primary quantities:

A = 8 E = 1.5217 I = 9.1217

B = 36 F = 38.7033 J = 30.7673

C = 3.1149 G = 8.4491 L = 156.6085

D = 12.0513 H = 3.2151

From these the secondary expressions are:

M = 17.2426 S = –5.4588

P = –15.7260 T = –21.2772

$Q = 2.4710$
$R = .5973$

$U = 145.2452$
$V = -9.1077$

Inserting in equations 10A and 11A we get

$$\alpha = (2.4710 \times -5.4588) - (-15.7260 \times .5973) = -4.0956 \text{ and}$$

$$D_k(\alpha) = (2.4710 \times 145.2452) + (.5973 \times -5.4588) - (-15.7260 \times -21.2772) = 21.0351$$

The estimate of the correction required in k is therefore given by

$$-\frac{\alpha}{D_k(\alpha)} = -\frac{-4.0956}{21.0351} = +.1947$$

and the estimated value k_2 is now given by

$$k_2 = k_1 - \frac{\alpha}{D_k(\alpha)} = .3000 + .1947 = .4947.$$

An improved estimate k_3 is now obtained by inserting the slightly rounded value $k_2 = .495$ and determining the primary and secondary quantities with the following results, working to one further place of decimals:

$A = 8$
$B = 36$
$C = 1.91691$
$D = 6.75650$
$M = 13.44504$
$P = -14.95676$
$Q = 2.19138$
$R = -1.44206$

$E = .73324$
$F = 18.52244$
$G = 4.38820$
$H = 1.23173$
$S = 9.79568$
$T = -2.94904$
$U = 33.06808$
$V = -23.52984$

$I = 2.64500$
$J = 13.57014$
$L = 65.19914$

From these we get

$$\alpha = -.10249$$

$$D_k(\alpha) = 14.23069$$

and therefore

$$k_3 = .495 - \frac{-.10249}{14.23069} = .495 + .0072 = .5022.$$

Using this value we can obtain a further estimate

$$k_4 = .5022 - \frac{.001269}{13.60655} = .5022 - .00009 = .50211.$$

Thus, although k_1 was rather badly chosen in the first place, the first corrected estimate (k_2) was within 1.5% of the true value and the next (k_3) within .02%.

For many practical purposes it is probably often unnecessary to go beyond the k_2 stage provided that k_1 is reasonably well chosen.

We can now proceed to derive t_0 and L_∞. Substituting in equation 13A provides an estimate of t_0. The best estimate of k is .5021 and should be used for this purpose, but the numerator can only be determined directly for $k = .5022$, and is

$$\log_e(-P) - \log_e(M) = 2.70021 - 2.58566 = .11455.$$

The correction for $k = .5021$ is derived from equation 15A and equals

$$(k_4 - k_3)\frac{(SM - PV)}{PM}$$

$$= (.5021 - .5022)\frac{[(10.02036)\ (13.27174) - (-14.88288)\ (-23.49246)]}{(-14.88288)\ (13.27174)}$$

$$= -.0001 \times 1.09130 = -.00011.$$

The best estimate of $\log_e(-P) - \log_e(M)$ is therefore

$$.11455 - .00011 = .11444$$

and therefore

$$t_0 = \frac{.11444}{.5021} = .22792.$$

L_∞ can now be derived. Inserting the values corresponding to $k = .5022$ in equation 16A we get

$$L_\infty = \frac{13.27174}{2.16983} = 6.11648.$$

If it is desired to obtain the even more accurate value corresponding to $k = .5021$, we use equation 17A, giving

$$D_k(L_\infty) = \frac{2.16983\ (-23.49246) - 2 \times 13.27174\ (-1.46082)}{2.16983^2} = -2.66249.$$

The required correction is therefore

$$(.5021 - .5022)\ (-2.66249) = .00027$$

and finally $L_\infty = 6.11648 + .00027 = 6.11675$.

If it should be believed that a biologically satisfactory solution is obtained by putting $t_0 = 0$, k is evaluated by taking the same preliminary estimate (.300), and using the same primary and secondary quantities and substituting in equations 19A and 20A giving

$$\beta = -15.7260 + 17.2426 = 1.5166$$

and $D_k(\beta) = -5.4588 - 9.1077 = -14.5665$.

Therefore $k_2 = .300 - \dfrac{1.5166}{-14.5665} = .4041$.

Using the rounded estimate of $k = .400$, we get

$$\beta = -15.68816 + 15.61396 = -.07420 \text{ and}$$

$$D_k(\beta) = 5.00504 - 21.19471 = -16.26387.$$

Therefore $k_3 = .400 - \dfrac{-0.7420}{-16.26387} = .400 - .0046 = .3954$.

A check at the next stage shows that this value is correct to four figures.

Estimation of L_∞ is as before: for $k = .400$

$$L_\infty = \frac{15.61396}{2.42234} = 6.44581.$$

Adjusting for $k = .3954$

$$D_k(L_\infty) = \frac{2.42234\ (-21.19471) - 2 \times 15.61396 \times (-.88972)}{2.42234} = -4.01461.$$

Therefore

$$\text{adjusted } L_\infty = 6.44581 + (.3954 - .4000)\,(-4.01461) = 6.46428.$$

Fiducial limits for L_∞, t_0 and k can now be calculated by the method outlined above using the values of the various expressions computed for $k = .5022$. The additional quantities required are

$$\Sigma l^2 = 176 \qquad\qquad Z = 1.1213$$

Then from equation 28, $s^2 = \dfrac{176 - 162 - 12.76020}{5} = .2480.$

Substituting in equation 24 gives

$$a_1 = 8.0 + (1.1213)^2 \times .7156 - 2.0 \times 1.1213 \times 1.8854 = 4.6717,$$

$$b_2 = (6.1165 \times .5022 \times 1.1213)^2 \times .7156 = 8.4892,$$

$$c_3 = (6.1165 \times 1.1213)^2\,(.2281^2 \times .7156 - 2 \times .2281 \times 1.1940 + 2.5418) = 95.6885,$$

$$P = a_2 = b_1 = 6.1165 \times .5022 \times 1.1213\,(1.1213 \times .7156 - 1.8854) = -3.7298,$$

$$q = b_3 = c_2 = 6.1165^2 \times .5022 \times 1.1213^2\,(.2281 \times .7156 - 1.1940) = -24.3495,$$

$$r = a_3 = c_1 = 6.1165 \times 1.1213\,[.2281 \times 1.1213 \times .7156 - 1.1213 \times 1.1940 - .2281 \times 1.8854 + 4.2914] = 18.5553,$$

and hence, from equation 30,

$$\Delta = 4.6717 \times 8.4892 \times 95.6885 + 2 \times 3.7298 \times 24.3495 \times 18.5553 - 4.6717 \times 24.3495^2 - 8.4892 \times 18.5553^2 - 95.6885 \times 3.7298^2 = 141.4102.$$

The estimates of the variances are therefore

$$\hat{V}(L_\infty) = \frac{8.4892 \times 95.6885 - 24.3495^2}{141.4102} \times .2480 = .3848,$$

$$\hat{V}(t_0) = \frac{95.6885 \times 4.6717 - 18.5553^2}{141.4102} \times .2480 = .1801, \text{ and}$$

$$\hat{V}(k) = \frac{4.6717 \times 8.4892 - 3.7298^2}{141.4102} \times .2480 = .04515.$$

For .05 confidence limits and 5 degrees of freedom, $t = 2.571$. The ranges for estimates are therefore

$$L_\infty = 6.1165 \pm 2.571\sqrt{.3848} = 4.5218 - 7.7112,$$

$$t_0 = .2281 \pm 2.571\sqrt{.1801} = -.8630 - 1.3192, \text{ and}$$

$$k = .5022 \pm 2.571\sqrt{.04515} = -.0441 - 1.0485.$$

In the above example, to illustrate the method the procedure has been followed to a level of accuracy well beyond that required for most ordinary purposes or that justified by the data. It is probable that in many cases, provided the trial value (k_1) of k is well chosen, the first approximation (k_2) will be close enough for practical needs. However, the adjustment procedure for t_0 and L_∞, using equations 15A and 17A, would not be satisfactory unless k_1 was close to the correct value. It would then be necessary to recalculate the various primary and secondary quantities for $k = k_2$ for this purpose, and, this being so, an improved estimate of k is easily obtained, and t_0 and L_∞ adjusted for this.

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Swimming Speeds of Sockeye and Coho Salmon on Spawning Migration[1,2]

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ABSTRACT

The speed at which sockeye and coho salmon swim while on spawning migration through a river was determined by direct timing of individual fish over measured river sections and by measurement of opposing water velocities. Migration was accomplished by two locomotory patterns: dart and steady swimming. For steady swimming there was a critical opposing water velocity from 1.1 to 1.7 ft/sec (mean 1.4 ft/sec). Against currents slower than the critical range steady swimming to a maximum speed of approximately 3.4 ft/sec (1.7 body lengths (L)/sec) was sustained through the observation areas, but against currents faster than the critical range salmon broke into position-holding behaviour at intervals. The calculated inter-decile range of swimming speeds (excluding slowest 10% and fastest 10%) against water velocities below the critical range was 1.75–3.18 ft/sec (0.9–1.7 L/sec) for sockeye salmon and 1.70–3.14 ft/sec (0.9–1.7 L/sec) for coho salmon. These swimming speeds were below maximum sustained values which have been determined experimentally.

INTRODUCTION

The speed at which fish swim has been the subject of much research in recent years using experimental laboratory techniques, and of this work the results and reviews of Bainbridge (1958a, b, 1960, 1961, and 1962) merit special attention. According to Bainbridge, fish can sustain speeds of 3–4 body lengths per second (L/sec) for long periods without fatigue, and maximum speeds may attain 10 L/sec for short periods. Since sustainable swimming speeds appear to be a function of fish length, a figure of 4.2 L/sec (Bainbridge, 1962) is given as an estimate for fish comparable in size to adult sockeye and coho salmon.

During the course of an investigation of the migratory ecology and behaviour of Pacific salmon, genus *Oncorhynchus*, undertaken from 1957 to 1963, adult salmon were observed at many localities on spawning migration. It appeared that migratory behaviour could be divided into two patterns of dart and steady swimming, and the latter could either be sustained for long distances or alternated with position-holding. From the casual, although numerous, observations it did not appear that adult salmon approximating 2 ft in length were normally sustaining swimming at speeds derivable from Bainbridge's

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hypothesis, i.e. 6–8 ft/sec, even when allowance was made for the velocity of opposing currents.

Simultaneously with these field observations experimental studies on adult salmon (Brett, 1965) produced a 60-min maximum sustained swimming speed for adult sockeye, *O. nerka*, of 2.5 L/sec. This is lower than Bainbridge's general figures, but even so imply swimming speeds of about 5 ft/sec. Again the numerous field observations did not support this value as being the normal sustained swimming speed of salmon on migration.

Objective field data to show that experimentally derived potential speeds are actually sustained by wild fish swimming freely in their natural environments have not been available for salmon. Relevant information consists largely of anecdotes such as those mentioned by Bainbridge (1960). Many attempts though have been made to estimate fish migration speeds by tagging, timing peak movements, etc. Such data are not reliable estimates of swimming speeds as we do not usually know whether the fish swam continuously during the recording period, or rested, or engaged in other behaviour such as escape from predators, etc., while migrating.

A field study directly measuring salmon swimming speeds was, therefore, greatly needed to complement experimental results, and to demonstrate their relevance to such problems of fisheries management as migration control, net design, etc. This paper contributes to satisfying the need by presenting swimming speed data obtained by direct timing of Pacific salmon over measured distances while on spawning migration through a river.

LOCALE AND METHODS

This project was part of a field study centered on the Somass River watershed of Vancouver Island. A preliminary report (Ellis, 1962) included a description of the locale and working concepts.

The swimming speed data were obtained during 1959, 1960, 1961, and 1962 at two localities on the Sproat River, one of the two main salmon tributaries of the system. Species observed were sockeye, *O. nerka*, and coho, *O. kisutch*.

The first observation point, named Upper Sproat, was U-shaped in cross-section and was bounded downriver by a rapids and upriver by a pool (Fig. 1). The bottom of bedrock and scree provided a sufficient number of stable marks for measurement and mapping. Most migrants ascended the rapids by dart swimming and then held at Holding Place 1 (HP1). Eventually they moved by steady swimming to HP3 and HP4 before entering the pool. Migration was usually about 6 inches off bottom along the deepest channel. The fish were timed over the measured distances shown using a stopwatch, and from these data the migration speeds in feet per second were calculated. Opposing water velocities were then measured and added to migration speeds to derive swimming speeds.

The clear water of the river provided adequate visibility for accurate timing, and also ensured recognition of returning fish and repeat migrants, so that these could be eliminated from the recording.

The second observation point, named Lower Sproat, overlooked salmon spawning beds where the river was almost rectangular in cross-section (Fig. 2). Nevertheless there was a network of channels slightly deeper than the generally flat gravel bottom. Salmon migrated through this river section by steady swimming close to the bottom tending to keep to the most central deep channel. Some fish held in HP1, and returning and wandering fish were again easily identified and eliminated from the recordings. Swimming speeds were derived from migration speeds and water velocities as at the Upper Sproat observation point.

Water velocities were obtained in two steps. During each day's observations, surface velocities were measured by timing 10 surface floats drifting over the route followed by salmon migrants. A conversion factor was needed to convert surface velocities to water velocities against which migrants were swimming at 6 inches off bottom. This factor was obtained from surface and subsurface readings made by a scuba diver and topside observer using an Ott current meter.

The series of readings obtained gave a conversion factor of 0.5 (mean of 6 days observations = 0.53, SD ±0.09), and this factor has been applied to the original surface velocity measurements obtained by floats to derive relevant subsurface velocities.

Rates of sustained swimming by salmon appear to be temperature dependent (Brett et al., 1958). In this investigation water temperatures ranged from daily minima as low as 15.4 C to as high as 20.5 C, and daily maxima from as low as 16.9 C to as high as 23.3 C. Fish migrating through small rivers in summer are exposed to considerable temperature variation from day to day through the 24-hr cycle according to vagaries of the weather. In a field study of the type reported here, it is not practicable to follow and analyse temperature variations and their effect on activity correlates. The subject will be considered in a subsequent paper.

It is the custom to convert swimming speeds and related data into terms of body lengths per second. Estimates of the mean lengths of sockeye and coho from the Somass watershed have been supplied by the Department of Fisheries, Vancouver, B. C. They are 55.65 cm fork length for sockeye based on 306 specimens, and 54.4 cm eye–hypural length for coho based on 268 specimens.

The swimming speed data for 1960 presented in this paper were previously published (Ellis, 1962) using surface water velocities and are now corrected.

RESULTS

The basic data are presented in Tables I and II.

Table I shows the water velocities for HP3-1 and HP4-3 at different dates and the percentages of salmon holding at HP3 and HP4, respectively,

TABLE I. Percentages of salmon holding position at HP3 and HP4 at Upper Sproat River.

Date	Species	Water velocity at HP3-1 (*ft/sec*)	Total no. of salmon observed at HP3	Per cent holding at HP3[a]	Water velocity at HP4-3 (*ft/sec*)	Total no. of salmon observed at HP4	Per cent holding at HP4[a]
1960							
June 21	Sockeye	2.2	41	80	–	–	–
" 22	"	2.2	13	80	1.6	24	50
July 13	"	1.6	27	80	1.4	19	50
" 28	"	1.1	1	0	0.8	5	0
Aug. 15	Sockeye and coho	0.9	38	0	0.7	45	0
Sept. 5–6	Coho	1.0	10	0	0.8	13	0
1961							
June 2–3	Sockeye	2.5	18	22	1.6	13	38
" 12	"	2.5	10	20	1.6	9	33
" 25	"	2.1	107	32	1.6	89	11
July 8	"	1.7	251	2	1.2	260	1
" 16	"	1.6	111	4	1.1	111	0
" 19	"	1.6	30	7	1.1	30	0
" 30	"	1.0	287	0	0.7	287	0
Aug. 4–5	"	1.0	12	0	0.7	12	0
" 18–19	Sockeye and coho	0.7	79	0	0.5	79	0
" 27	" " "	0.7	65	0	0.5	65	0
1962							
Aug. 21	Sockeye and coho	1.4	43	12	0.9	43	0
" 27	" " "	1.1	48	8	0.8	48	0
Sept. 4	Coho	1.0	10	0	0.7	10	0
" 10	"	0.8	136	0	0.6	136	0
" 20	"	0.7	50	0	0.5	50	0

[a]Estimates only in 1960.

after swimming against these water velocities. During periods of high water velocities, which generally occurred during early sockeye runs, many migrants passing through Upper Sproat held position.

In 1960, holding ceased at HP3 and HP4 during the period July 13–28 and this coincided with drops in water velocity from 1.6 to 1.1 ft/sec at HP3-1 and 1.4 to 0.8 ft/sec at HP4-3.

In 1961, there was a progressive decrease through the summer in numbers holding, such that holding virtually ceased at HP3 from July 8 to 19 and at HP4 from June 25 to July 8. These periods coincided with drops in water velocity from 1.7 to 1.6 ft/sec at HP3 and 1.6 to 1.2 ft/sec at HP4.

In 1962, heavy summer rains kept Sproat River discharges high such that relatively fast water velocities at HP3-1 (1.4–1.1 ft/sec) in August were accompanied by some holding.

At Lower Sproat water velocities were not recorded above 1.6 ft/sec and holding did not normally occur during peak migration periods. (Holding did

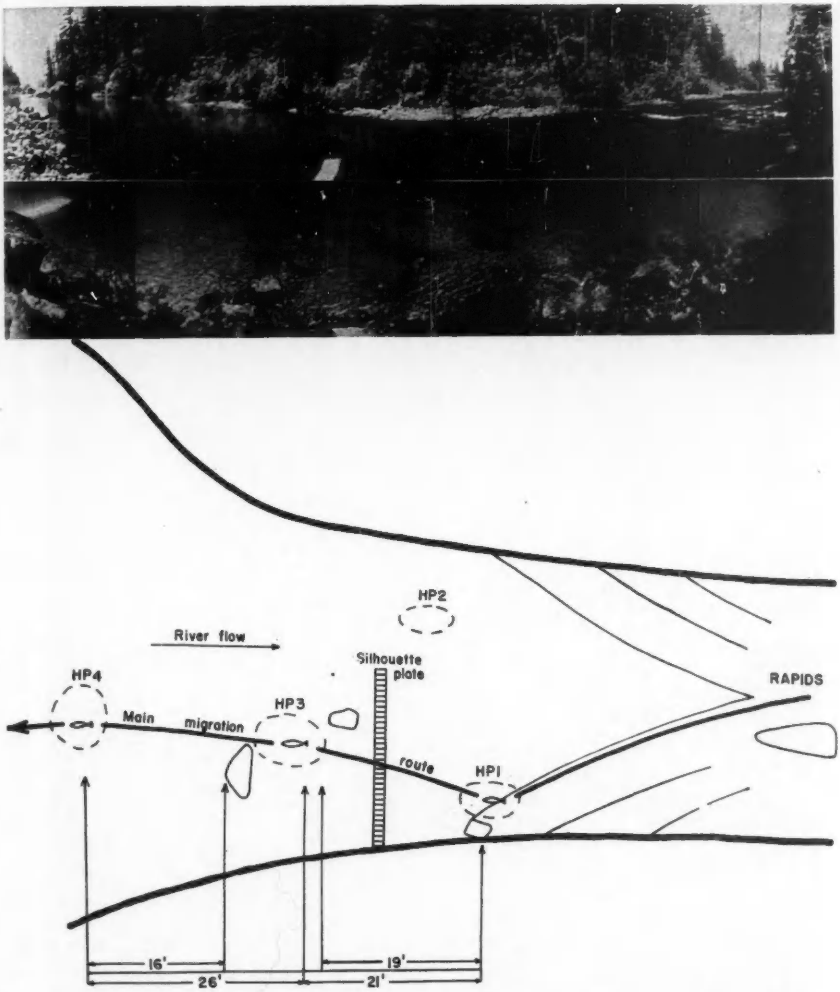
HP2
River flow
Silhouette plate
HP4
RAPIDS
Main migration route
HP3
HP1
16'
19'
26'
21'

FIG. 1. The Upper Sproat observation point. *Top.* Panorama from the south bank showing on the left the line formed from junction of scree and bedrock coinciding with the deepest channel leading upriver to a pool, and on the right the rapids leading downriver. The white silhouette plate is at the centre. *Middle.* Underwater panorama showing bedrock bottom at HP1 (centre) with silhouette plate at left. *Bottom.* Plan of measured area showing distances used for timing and main route followed by migrants.

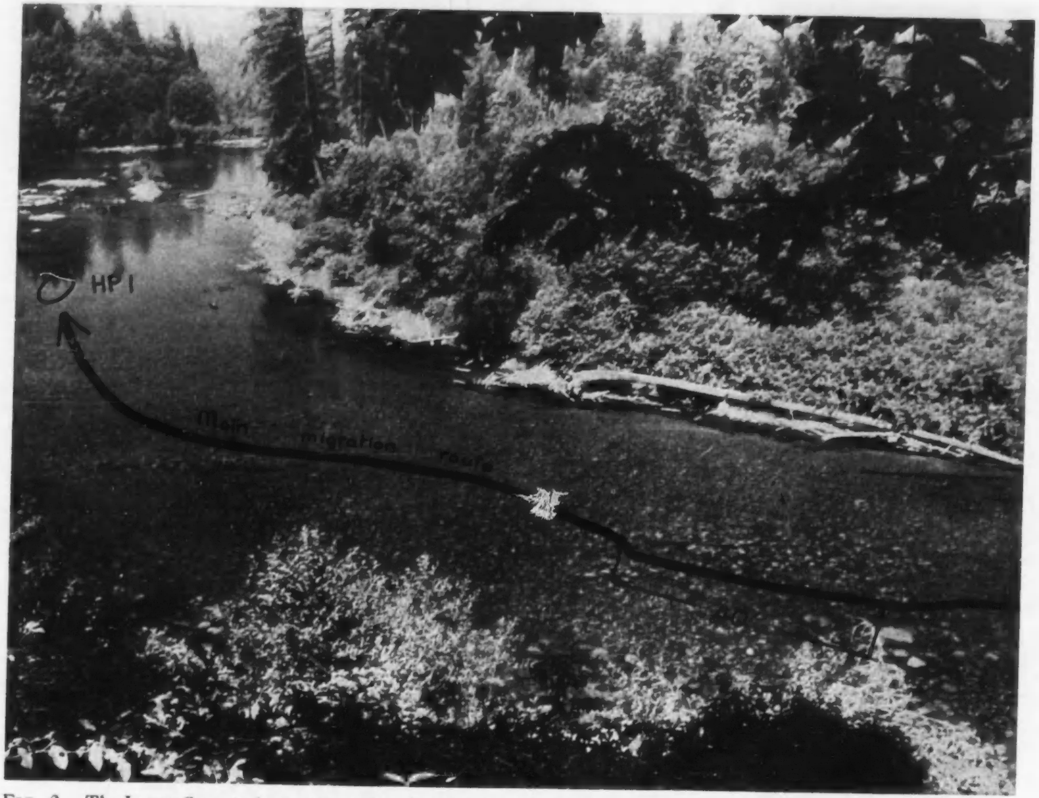
HP1
Main migration route

FIG. 2. The Lower Sproat observation point showing the almost flat gravel bottom, main migration route, measured section, and upriver holding place (HP1).

TABLE II. Results of swimming speed calculations at Upper Sproat River.

	Measured distance HP1-3 (1960—21 ft; 1961 and 1962—19 ft)				Measured distance HP3-4 (1960—26 ft; 1961 and 1962—16 ft)			
Date	No. salmon timed	Migration speed (*ft/sec*)		Swimming speed (*ft/sec*)	No. salmon timed	Migration speed (*ft/sec*)		Swimming speed (*ft/sec*)
		Mean value	Standard deviation			Mean value	Standard deviation	
SOCKEYE								
1960								
June 21	41	1.1	0.31	3.3	–	–	–	–
" 22	13	1.1	0.46	3.3	23	1.1	0.30	2.7
July 13	27	1.1	0.33	2.7	19	1.3	0.35	2.7
" 28	1	0.6	–	1.7	5	2.0	0.73	2.8
Aug. 15	35	1.2	0.39	2.1	31	2.2	0.73	2.9
1961								
June 2–3	3	2.0	0.35	4.5	11	1.1	0.41	2.7
" 12	7	1.9	0.23	4.4	7	1.0	0.32	2.6
" 25	40	1.9	0.71	4.0	41	1.1	0.42	2.7
July 8	73	1.7	0.54	3.4	89	1.2	0.41	2.4
" 16	38	1.7	0.56	3.3	40	1.1	0.29	2.2
" 19	19	1.8	0.74	3.4	19	1.3	0.35	2.4
" 30	54	1.6	0.48	2.6	61	1.2	0.30	1.9
Aug. 4–5	6	1.9	0.51	2.9	8	1.4	0.37	2.1
" 18–19	28	2.5	0.77	3.2	36	1.8	0.55	2.3
" 27	24	2.0	0.76	2.7	26	1.5	0.39	2.0
1962								
Aug. 21	1	1.8	–	3.2	1	2.1	–	3.0
" 27	3	1.6	0.16	2.7	4	1.2	0.57	2.0
COHO								
1960								
Aug. 15	5	1.4	0.70	2.3	5	2.0	1.11	2.7
Sept. 5–6	10	1.2	0.26	2.2	13	2.3	0.51	3.1
1961								
Aug. 18–19	8	2.8	1.30	3.5	14	1.7	0.56	2.2
" 27	11	2.0	1.24	2.7	14	1.5	0.45	2.0
1962								
Aug. 21	4	1.8	0.56	3.2	4	1.2	0.22	2.1
" 27	13	1.8	0.58	2.9	15	1.2	0.50	2.0
Sept. 4	2	1.9	0.50	2.9	4	1.0	0.37	1.7
" 10	34	1.5	0.34	2.3	35	1.4	0.28	2.0
" 20	18	1.7	0.47	2.4	19	1.5	0.31	2.0

occur at off-peak periods, but evidence to be presented in another paper suggests that it was the result of a diel activity cycle.)

We can now see that where opposing water velocities dropped through the range 1.7–1.1 ft/sec (mean 1.4 ft/sec) there was behavioural change in manner of swimming, in that nonsustained steady swimming gave way to sustained steady swimming. This range of opposing water velocities appears to be critical for the maintenance of steady swimming.

Table II shows mean migration speeds for salmon timed through Upper Sproat Observation Point. The Table shows the numbers of fish timed and calculated swimming speeds based on water velocity data in Table I. Faster swimming is needed to pass through higher velocity water early in each season as is to be expected. The maximum mean recorded was 4.5 ft/sec against a water velocity of 2.5 ft/sec and the minimum mean 1.7 ft/sec against a water velocity of 0.7 ft/sec. Standard deviations shown in Table II for migration speeds reflect the considerable spread in the data resulting from skewness towards faster speeds. At Lower Sproat Observation Point, 19 fish timed during the 3 years of observations showed speeds within the range shown at Upper Sproat.

Analysis of variance was used to test the hypothesis that fish during various observation periods were maintaining similar swimming speeds against water velocities below the critical range. Such tests in various groupings indicated significant differences presumably arising through the many environmental factors known to or probably affecting swimming speeds, e.g. water temperatures, state of maturity, etc. A combined mean for these swimming speeds therefore has little biological significance.

Table III shows the ranges of swimming speed means for samples of sockeye at Upper Sproat grouped for fish swimming against flows higher, within, and below the critical range. Quite obviously, again, faster swimming speeds are necessary against faster flows but there are two meaningful ranges included in the Table. The range of values 2.4–3.4 ft/sec against water flows within the critical velocity range indicates swimming speeds at levels where position-holding is occasionally induced. The minimum value of 3.3 ft/sec for swimming speeds against water flows above the critical range is virtually identical with the maximum swimming speed values within and below the critical flow range. These values 3.2–3.4 ft/sec (1.6–1.7 L/sec) appear to be biologically significant swimming speeds. When these sockeye and coho salmon

TABLE III. Relationship between range of swimming speed mean values for sockeye at the Upper Sproat critical water velocity range (1.1–1.7 ft/sec) and amount of position-holding.

Water velocity	Amount of position-holding	Range of mean swimming speeds (*ft/sec*)
Greater than critical range	Much	3.3–4.5
Within critical range	Little	2.4–3.4
Less than critical range	None	1.7–3.2

swam steadily at a speed above these values the swimming was not sustained indefinitely, whereas at speeds below these values steady swimming was sustained through the observation areas.

Frequently distributions for individual swimming speeds on any one day were skewed towards higher values. The inter-decile range, excluding slowest 10% and fastest 10%, provides an indication of more regularly attained swimming speeds than does the range itself. The calculated inter-decile range of sustained swimming speeds for individual sockeye was 1.75–3.18 ft/sec with an actual range of 1.3–5.2 ft/sec. This latter approximates speeds achieved in dart swimming. The calculated inter-decile range of sustained swimming speeds for individual coho was 1.70–3.14 ft/sec with an actual range of 1.0–5.3 ft/sec.

Expressed in terms of body lengths per second the range of sustained swimming speeds usually exhibited was 0.9–1.7 L/sec for both sockeye and coho. The maxima in these ranges agree with the values obtained earlier at 1.7 L/sec above which salmon break into position-holding behaviour. Furthermore, both sets of data are considerably lower than the experimentally derived values for sustained swimming quoted by Bainbridge (1960), i.e. 3–4 L/sec. They are also less than the speed of 2.5 L/sec derived from sockeye experimental material (Brett, 1965).

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Free-Swimming Copepod Nauplii of Narragansett Bay with a Key to Their Identification[1,2]

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ABSTRACT

Zooplankton surface samples were taken with a number 12 silk bolting cloth net towed by a Clark-Bumpus quantitative plankton sampler in Narragansett Bay for 12 months. The samples were collected twice weekly, except during December, January, and February, at night at one position in the West Passage of Narragansett Bay. Ten calanoid, three cyclopoid, and one harpacticoid species of free-swimming copepod nauplii were collected from July 1957 through June 1958. The structure and arrangement of elements of the caudal armatures of these copepod nauplii showed certain differences which were utilized to develop a key.

INTRODUCTION

Numerous investigations have determined that copepods, predominantly developmental stages, comprise the greatest number of zooplankters throughout most of the year in open coastal waters. Copepod nauplii are the most abundant and small pelagic fish, comb jellies, arrow worms, and others are probably dependent upon them for survival.

Based on the ease in viewing and differences of structure and arrangement of the caudal armature elements, a key to the copepod nauplii of Narragansett Bay was developed. This key will aid planktologists in the identification of free-swimming nauplii occurring in Narragansett Bay and other northeastern Atlantic waters with a similar copepod fauna. Because of emphasis on the caudal armatures, other parts of the nauplius are not considered in this paper except in the case of *Hemicyclops adhaerens* (Williams).

The adult copepods from Narragansett Bay, Rhode Island, have been described (Wilson, 1932a; Davis, 1944) and there is a key to a few of their nauplii (Oberg, 1906). Oberg's key includes such minute anatomy as spines on the mandibles and antennae and for this reason his key is difficult to use for surveys, when identification must necessarily be rapid. Because the copepodid stages are morphologically similar to the adults, it is the nauplii that are in need of attention.

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METHODS

Narragansett Bay is a 100 square mile estuarine area in Rhode Island. According to Hicks (1959), the Bay can be considered as a Prichard type B estuary (type 2, Stommel and Farmer) with a nontidal flow out of the Bay at the surface and in at the bottom. Conanicut, Prudence, and Aquidneck Islands divide the Bay into its three principal channels: the West Passage, the East Passage, and the Sakonnet River. The water in the West Passage from which the samples were collected can be classified according to the "Venice System" (International Association of Limnology, 1958) as (mixo) polyhaline within the mixo-haline zone. The surface salinity during the period of collection ranged from 27.5 to 32.4‰ (Hicks, 1963) and the annual temperature range was 18 C (Faber, 1959).

Zooplankton surface samples were taken with a number 12 silk bolting cloth net towed by a Clark-Bumpus quantitative plankton sampler. They were taken from a 12-ft rowboat powered by a 5-hp motor at a speed of about 0.5 knot. The samples were collected at night at least ½ hr after dark at one position (71°25′W long, 41°30′N lat) in the West Passage of Narragansett Bay between July 1957 and June 1958. Samples were taken twice weekly except during December, January, and February when stormy weather made the Bay hazardous and then they were taken as often as possible. The hauls ranged from 5 to 15 min in length and the samples were preserved in 3% formalin–sea water solution.

Two 1-ml aliquots from each sample were put into a Lucite counting chamber and all nauplii examined. Unidentifiable nauplii were drawn with the aid of a camera lucida, counted, and correlated with the copepodids present in the aliquots. In this way the nauplii of *Eurytemora herdmani* Thompson and Scott, *Hemicyclops adhaerens* (Williams), *Labidocera aestiva* Wheeler, *Paracalanus crassirostris* Dahl, and *Pseudodiaptomus coronatus* Williams were identified. Identification of *Hemicyclops adhaerens* (Williams) was not certain because no description of nauplii of any species of *Hemicyclops* has been published. No attempt was made to hatch eggs from ovigerous females of any species.

IDENTIFICATION

KINDS OF NAUPLII COLLECTED

Ten calanoid, three cyclopoid, and one harpacticoid species of free-swimming copepod nauplii, representing eight genera, were collected (Table I). In addition to the 14 species of nauplii observed in the samples, there were unidentifiable early-stage nauplii, small numbers of benthonic harpacticoid forms, and scattered representatives of semi-parasitic and/or parasitic nauplii. The harpacticoid nauplii are crawling benthonic forms and are collected irregularly with a plankton net. Identification of the few semi-parasitic nauplii was not possible because very few have been described (presumably most were Poecilostoma).

TABLE I. Checklist of copepods from Narragansett Bay which have free-swimming naupliar instars and their seasonal occurrence from July 1957 to June 1958. Classification taken from G. O. Sars (1903).

	Months observed in West Passage
CALANOIDA	
Amphascandria	
Paracalanidae	
Paracalanus crassirostris Dahl	July–December
Pseudocalanidae	
Pseudocalanus minutus Krøyer	November–July
Heterarthrandria	
Centropagidae	
Centropages hamatus (Lilljeborg)	All except September
Temoridae	
Temora longicornis (O. F. Müller)	December–July
Eurytemora americana Williams[a]	None
Eurytemora herdmani Thompson and Scott	May–July
Eurytemora hirundoides (Nordquist)[b]	None
Pseudodiaptomidae	
Pseudodiaptomus coronatus Williams	July–November
Pontellidae	
Labidocera aestiva Wheeler	July–November
Acartiidae	
Acartia clausi Giesbrecht	November–June
Acartia tonsa Dana	June–January
Tortanus discaudatus (Thompson and Scott)	March–July
Tortanus setacaudatus Williams[c]	None
CYCLOPOIDA	
Gnathostoma	
Oithonidae	
Oithona brevicornis Giesbrecht	July–December ?
Oithona similis Claus	All months ?
Poecilostoma	
Clausidiidae	
Hemicyclops adhaerens (Williams)	September–October, May–June
HARPACTICOIDA	
Achirota	
Longipediidae	
Longipedia helgolandica Klie	May–November

[a] Not included in key. Found by Williams (1907) in Narragansett Bay but not by Frolander (MS, 1955) or the present study.

[b] Collected in Greenhill Pond and estuaries leading into Narragansett Bay. Possibly *E. hirundoides* is a variety of *E. affinis* (see footnote 4).

[c] Collected in Greenhill Pond.

Many naupliar instars would ordinarily be regarded as metanauplii, but modern copepodologists usually consider all of the pre-copepodid instars as nauplii because of their morphological similarity. The term nauplius has been retained in this paper for all these instars.

The nauplii collected are from copepods with two different life histories. The majority are free-swimming throughout their active period while the other kind, usually known as semi-parasitic, are free-swimming only during the naupliar instars and sometimes as early copepodids (Snodgrass, 1956).

The typical life stages of a free-swimming copepod consist of an egg, six naupliar instars, and six copepodid instars of which the last is the adult. These 12 active stages are free-swimming and rarely, if ever, alight on aquatic plants or floating debris. The typical life stages of a semi-parasitic species consist of an egg, five or less naupliar instars, and five or less copepodid instars of which the last is the adult. Their nauplii are free-swimming but upon molting to the copepodid instar there is a movement towards the bottom in search of a favorable surface or host if it is one of the many species that live in association with other animals. Only *Hemicyclops adhaerens* (Williams) and *Longipedia helgolandica* Klie have the latter kind of life history.

The length of time that any copepod remains a nauplius is quite variable and depends upon the environmental conditions and physiology of the individual. Marine copepods are difficult to raise in the laboratory and little information is available on this aspect. Kogo (1960), however, reported that fast-growing nauplii of *Centropages abdominalis* Sato, a shallow-water coastal marine species, became Nauplius VI in 10 days in the laboratory at 15.4 C. The duration of each instar ranged from 1 to 4 days.

Morphology of the Naupliar Caudal Armature

The morphology of various types of crustacean nauplii is well documented (Snodgrass, 1956), but the caudal armatures have never been utilized as a sole means of identification. Lindquist (1959) utilized the antennule in addition to the caudal armature in describing the developmental stages of *Limnocalanus grimaldi* (de Guerne). Distinct differences, including caudal armatures, exist between the instars of a single species. Commonly Nauplius I is devoid of any caudal armature and at this stage one species is practically indistinguishable from another.

Differences in caudal armature arrangements are usually less between species than between genera. Johnson (1935) found very little difference in the caudal armatures of two west coast marine species of *Labidocera* and states that "during the second to sixth nauplius stages and during the first copepodid stage they are separable only by small but yet definite specific characters, the most useful of these being the type of masticatory hook occurring on the second basipod of the second antenna." Figures in the present account indicate that other genera, such as *Tortanus*, show considerably more variation in caudal armatures. The problem of specific differences becomes more involved when freshwater copepods are considered, since there are so many species of *Diaptomus* and *Cyclops*. Dukina (1956), nevertheless, claims that the nauplii of different species of *Cyclops* can be identified by careful observation of structural details, including (a) size, form, and location of the elements of the caudal armature, (b) relative lengths of the segments of the first antennae, (c) pattern of small hairs on the abdomen, and (d) shape and armature of the labium, second antennae, and mandibles.

The terminology for caudal armatures is not uniform in the literature and a generally acceptable one will be difficult to establish because of the great variety of elements. In this paper all elements arising from the posterior end are considered the caudal armature. A "spine" is defined as a more or less inflexible element which tapers throughout its length, while a "seta" is flexible and usually thinner than a spine with edges appearing parallel for most of its length. The posterior end of the body is sometimes separated by a cleft into two lateral caudal lobes.

Naupliar morphology has rarely been used in systematic or ecological studies of copepods so it is suggested that a ventral view and if necessary a lateral view of the last nauplius be included in species descriptions. Figure 32 shows the oldest nauplius of *Hemicyclops adhaerens* in the suggested view.

CAUDAL ARMATURES OF PREVIOUSLY DESCRIBED NAUPLII

Of the 14 species of copepod nauplii collected and identified from Narragansett Bay in this study, seven have been described previously from other localities. Caudal armatures of representative stages of six of these have been redrawn from the literature. The caudal armature of *Tortanus discaudatus* (Thompson and Scott) collected in Narragansett Bay showed enough differences from published illustrations to justify new drawings. In order to have a more complete list of species which have been recorded in the Bay previously, *Eurytemora hirundoides* (Nordquist)[4] was also included. Figures 1–16 show caudal armatures of previously described nauplii.

Oberg (1906) was one of the earliest workers on copepod development. Collecting in Kieler Bucht, he identified and illustrated the naupliar instars of four copepod species whose geographical ranges extend into Narragansett Bay. Davis (1943) described all of the naupliar instars of *Eurytemora hirundoides* (Nordquist) from Chesapeake Bay. Conover (1956) did a thorough job of separating and describing the nauplii of *Acartia clausi* Giesbrecht and *A. tonsa* Dana of Long Island Sound.

Although the general shape and structure of the nauplius of *Tortanus discaudatus* (Thompson and Scott) from Narragansett Bay is similar to Johnson's (1934) description of the Pacific form, there are distinct differences between the caudal armatures of the two forms. Original drawings of the caudal armatures from Narragansett Bay specimens are presented. The early-stage nauplius of *T. discaudatus* from Narragansett Bay (Fig. 15) has two caudal setae, one slightly stouter and longer than the other. Several setae are added during development. In Nauplius VI (Fig. 16) there are five caudal setae, with the left median seta curved dorsally. Elements of the caudal armature of the Pacific form as drawn by Johnson (1934) are shorter and more spine-like than those of the Atlantic form. A prominent pair of plumose setae are absent from the Atlantic form.

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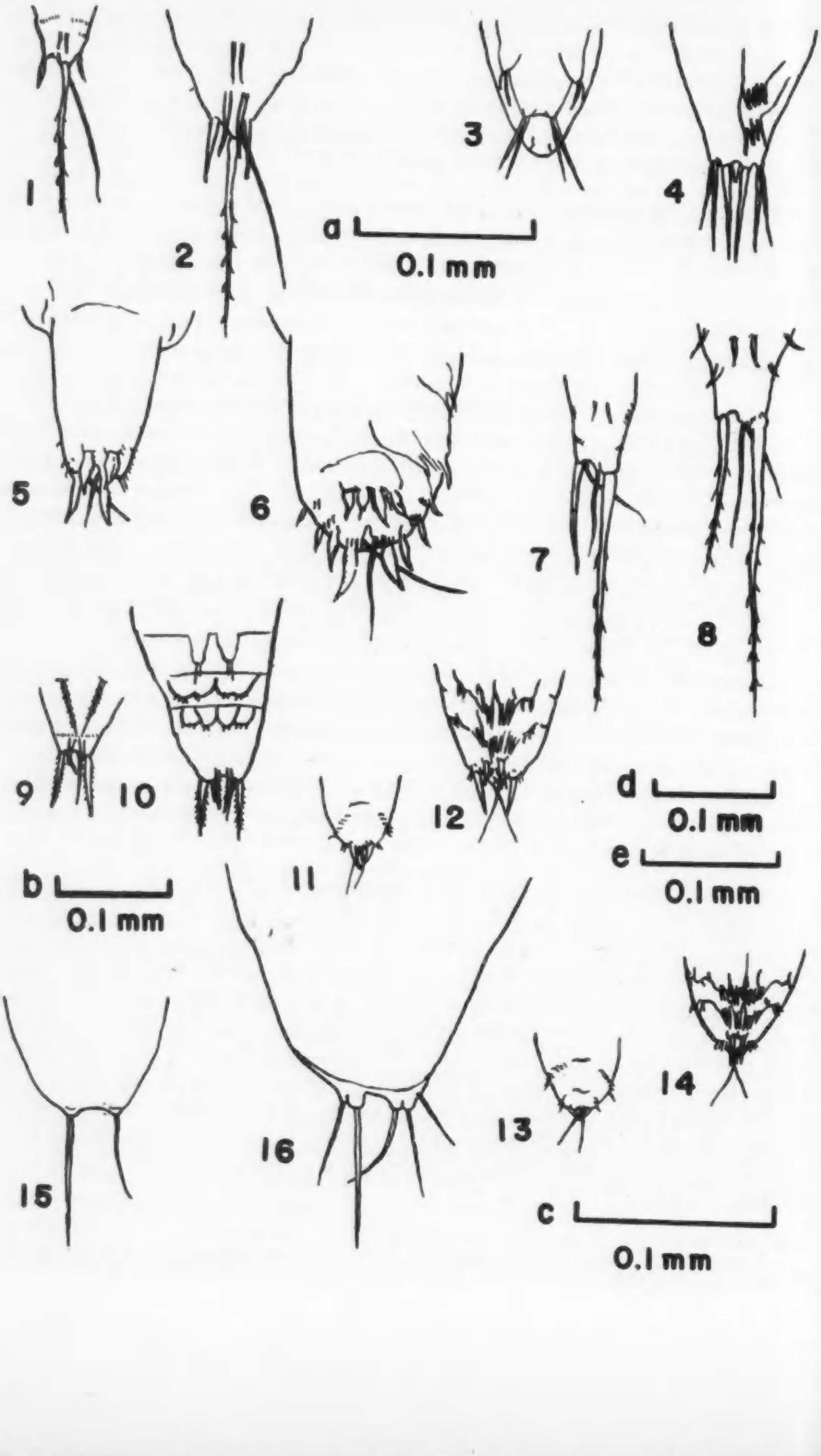
[4] This species may be *E. affinis* (Poppe) for Jeffries (personal communication) indicates that his report of *E. hirundoides* in two Rhode Island estuaries (Jeffries, 1962) was *E. affinis*.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CAUDAL ARMATURES OF UNDESCRIBED NAUPLII

Based on past published records of adult copepods collected in the Narragansett Bay region (Table I), there are nine undescribed nauplii. Original illustrations of the caudal armatures of representative naupliar instars of the six following species are included: *Eurytemora herdmani* Thompson and Scott, *Labidocera aestiva* Wheeler, *Longipedia helgolandica* Klie, *Oithona brevicornis* Giesbrecht, *Paracalanus crassirostris* Dahl, and *Pseudodiaptomus coronatus* Williams. *Tortanus setacaudatus* Williams is included because of its presence in nearby Greenhill Pond and close taxonomic relationship to *T. discaudatus*. Besides the caudal armatures of representative naupliar instars of *Hemicyclops adhaerens*, details of its body shape and appendages are included. Developmental stages of *Eurytemora americana* Williams could not be obtained.

EURYTEMORA HERDMANI

The nauplii of three other species of *Eurytemora* are illustrated in the literature. Naupliar stages of *Eurytemora hirundoides* (Nordquist) were described by Davis (1943) and those of *E. velox* Lilljeborg by Gurney (1931). Three naupliar instars of *E. hirundo* Giesbrecht were described by Oberg (1906). The posterior of *E. herdmani*'s nauplius appears more slender than the other described species with the caudal spines more asymmetrical.

In the caudal armature of *E. herdmani* Thompson and Scott (Fig. 17 and 18) the left spine is longer and stouter throughout its development than *E. hirundoides* (Fig. 9 and 10), but Davis (1943) mentions that even *E. hirundoides* has the left spine slightly longer. The caudal armature of *E. velox* has the left spine distinctly longer than the right. In Nauplius VI of *E. herdmani* the right medial seta, absent from earlier instars, is curved dorsally.

LABIDOCERA AESTIVA

Nauplii of three species of *Labidocera* have been described. Johnson (1935) described the naupliar instars of *L. jollae* and *L. trispinosa* from coastal waters of the Pacific Ocean and Krishnaswamy (1950) has illustrated a dorsal view of an early-stage nauplius of *Labidocera* sp. from coastal waters near Madras in

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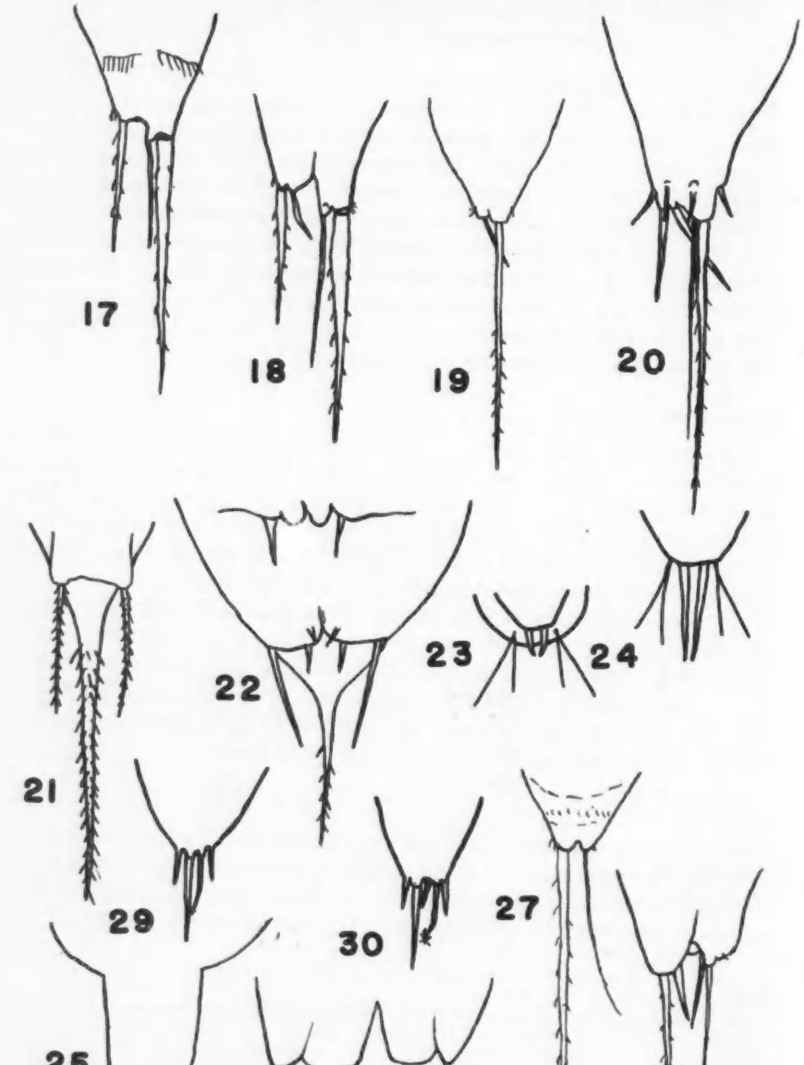
FIG. 1–16. Caudal armatures of previously described copepod nauplii. Scale *a* applies to 1–8; *b* to 9 and 10; *c* to 15 and 16; *d* to 11 and 13; and *e* to 12 and 14. **1.** *Centropages hamatus* (Lilljeborg) Nauplius III (redrawn from Oberg, 1906). **2.** *Centropages hamatus* (Lilljeborg) Nauplius VI (redrawn from Oberg, 1906). **3.** *Oithona similis* Claus Nauplius III (redrawn from Oberg, 1906). **4.** *Oithona similis* Claus Nauplius VI (redrawn from Oberg, 1906). **5.** *Pseudocalanus minutus* Krøyer Nauplius III (redrawn from Oberg, 1906). **6.** *Pseudocalanus minutus* Krøyer Nauplius VI (redrawn from Oberg, 1906). **7.** *Temora longicornis* (O. F. Müller) Nauplius III (redrawn from Oberg, 1906). **8.** *Temora longicornis* (O. F. Müller) Nauplius VI (redrawn from Oberg, 1906). **9.** *Eurytemora hirundoides* (Nordquist) Nauplius III (redrawn from Davis, 1943). **10.** *Eurytemora hirundoides* (Nordquist) Nauplius VI (redrawn from Davis, 1943). **11.** *Acartia clausi* Giesbrecht Nauplius III (redrawn from Conover, 1956). **12.** *Acartia clausi* Giesbrecht Nauplius VI (redrawn from Conover, 1956). **13.** *Acartia tonsa* Dana Nauplius III (redrawn from Conover, 1956). **14.** *Acartia tonsa* Dana Nauplius VI (redrawn from Conover, 1956). **15.** *Tortanus discaudatus* (Thompson and Scott) early-stage (drawn from West Passage specimen). **16.** *Tortanus discaudatus* (Thompson and Scott) Nauplius VI (drawn from West Passage specimen).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the Indian Ocean. The latter nauplius differs from all others by lacking a long spine on the left side of the caudal armature, but it might easily have broken off without notice during collection. There is a greater difference between the caudal armature of the Atlantic Ocean species and either one of the Pacific Ocean species than there is between the two Pacific Ocean species.

The caudal armature of the early-stage nauplius of *L. aestiva* Wheeler (Fig. 19) is characterised by two spines, the left being about four times longer than the right. The distal half of the long left spine is plumose. The right spine of *aestiva* is shorter in comparison to the left than either that of *jollae* or *trispinosa*. The caudal armature of Nauplius VI (Fig. 20) has three spines and a single left seta. The two right spines are very similar in structure and length but the medial one is usually pointed towards the left side of the body. The right medial spine and left seta of the caudal armature of *jollae* and *trispinosa* are plumose but they are smooth in *aestiva*.

LONGIPEDIA HELGOLANDICA

Claus (1863) first recognized this larva as that of a copepod. *Longipedia coronata* Claus is the only species of *Longipedia* recorded from the North American coast (Wilson, 1932a), but González and Bowman (1965) believe that all published records from North America are *L. helgolandica* Klie. The nauplius collected in Narragansett Bay is morphologically different from Nicholls' (1935) description of the nauplius of *L. coronata*. The form from the Bay resembles that of *L. scotti* G. O. Sars in having a broad, rounded anterior margin rather than the helmet-shaped head characteristic of *L. coronata*. Based on the opinion of González and Bowman (1965) and the difference of the nauplius from that of *L. coronata*, I am tentatively referring this nauplius to *L. helgolandica* Klie. The copepodids are benthonic, hence identification will remain uncertain until the nauplius can be reared to the adult.

The nauplii of three species of *Longipedia* were described by Nicholls (1935). The caudal armatures of these species and the form collected in Narragansett Bay are similar. The early-stage nauplius (Fig. 22) has three plumose spines while the oldest nauplius (Fig. 22) has only one. It is not known how many naupliar instars the *Longipedia* from Narragansett Bay goes through to molt into a copepodid.

OITHONA BREVICORNIS

Oberg (1906) described all of the nauplii of *O. similis* Claus while Murphy (1923) described naupliar instars of *O. nana* Giesbrecht. Gibbons and Ogilvie

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Fig. 17–30. Caudal armatures of undescribed copepod nauplii. Figures 17–28 drawn from West Passage specimens; Figures 29 and 30 drawn from Greenhill Pond specimens. Scale *a* applies to 25; *b* to 17–24 and 26–30. **17.** *Eurytemora herdmani* Thompson and Scott early-stage. **18.** *Eurytemora herdmani* Thompson and Scott Nauplius VI. **19.** *Labidocera aestiva* Wheeler early-stage. **20.** *Labidocera aestiva* Wheeler Nauplius VI. **21.** *Longipedia helgolandica* Klie early-stage. **22.** *Longipedia helgolandica* Klie late-stage. **23.** *Oithona brevicornis* Giesbrecht early-stage. **24.** *Oithona brevicornis* Giesbrecht late-stage. **25.** *Paracalanus crassirostris* Dahl early-stage. **26.** *Paracalanus crassirostris* Dahl Nauplius VI. **27.** *Pseudodiaptomus coronatus* Williams early-stage. **28.** *Pseudodiaptomus coronatus* Williams Nauplius VI. **29.** *Tortanus setacaudatus* Williams early-stage. **30.** *Tortanus setacaudatus* Williams Nauplius VI.

(1933) compared the naupliar instars of *O. helgolandica* Claus and *O. spinirostris* Claus and indicated that the older instars were separable by their caudal armatures.

The general structure of the caudal armature of *O. brevicornis* Giesbrecht is similar to others described from nauplii of Cyclopoida. The caudal armature of the early-stage nauplius (Fig. 23) consists of a pair of spines arising from the ventral abdomen and two pairs of lateral setae. In the late-stage nauplius (Fig. 24) the spines have grown in length in comparison to the setae and now arise from the extreme caudal end.

PARACALANUS CRASSIROSTRIS

A developmental stage of *Paracalanus* was first described by Oberg (1906), who illustrated a Nauplius VI which he considered to be *P. parvus* Claus. Since then all of the naupliar instars of *P. parvus* have been described (Ogilvie, 1953). *Paracalanus crassirostris* Dahl is claimed by Davis (1944) to be the smallest calanoid copepod known and the size of the adult, of course, is reflected in its developmental instars.

The caudal armature of the early-stage nauplius of *P. crassirostris* Dahl is characterized by a single pair of short spines and a longer medial seta (Fig. 25). The body of the nauplius is conspicuously divided into a rounded anterior and a cylindrical abdomen-like posterior. In Nauplius VI (Fig. 26) the short spines are enlarged and a pair of lateral setae are added.

PSEUDODIAPTOMUS CORONATUS

Johnson (1948) indicates that the nauplius of the genus *Pseudodiaptomus* lies morphologically somewhere between *Diaptomus* and *Eurytemora* and that it may have its closest marine affinities with *Eurytemora*. All developmental stages of *Pseudodiaptomus euryhalinus* Johnson have been described by Johnson (1948) and Nauplius I of *P. aurivilli* has been described by Krishnaswamy (1950).

The caudal armature of the early-stage nauplius of *P. coronatus* Williams has a right plumose spine, and a shorter left seta (Fig. 27). In Nauplius VI the seta is a little longer than the plumose spine and there is a pair of medial spines, one of which is curved dorsally (Fig. 28). All of the three described species of *Pseudodiaptomus* are characterized by oversized labrums.

TORTANUS SETACAUDATUS

The nauplii of two other species of *Tortanus* have been described in the literature. The nauplius of *T. discaudatus* has been described from coastal waters of the Pacific Ocean by Johnson (1934) and two representative caudal armatures of Narragansett Bay nauplii are shown in Fig. 15 and 16. The difference in appearance between these two forms is discussed in an earlier section. Krishnaswamy (1950) has illustrated an early-stage nauplius of *T. gracilis* from coastal waters of the Indian Ocean. The gross anatomy of all the described forms is similar but the caudal armatures appear to be morphologically distinct.

I examined a plankton sample[5] containing developmental stages of *T. setacaudatus* Williams from Greenhill Pond, Rhode Island. The nauplius was identified by its abundance, size-relation to the copepodids of *T. setacaudatus*, and elimination of all the other common nauplii in the sample. Figures 29 and 30 show the caudal armatures of an early-stage nauplius and Nauplius VI as drawn from specimens from Greenhill Pond. They are unique in having a ventrally curved seta. The Narragansett Bay form of *T. discaudatus* has a seta curved dorsally. In developing from the early-stage instar to Nauplius VI the caudal armature shows the addition of a short medial spine and a conspicuous tuft of hairs at the tip of the ventrally curved seta.

NAUPLIUS OF *HEMICYCLOPS ADHAERENS*

I am tentatively referring this nauplius (Fig. 31–36) to *Hemicyclops adhaerens* (Williams), even though nauplii have not been hatched from eggs. In plankton samples these nauplii were always found in abundance with early copepodids[6] ("Saphirella stage") of *H. adhaerens* (Williams). This nauplius is assigned to this species because of the information concerning the identity of the copepodids given to me by Dr Gooding, because it is not exactly like any previously described nauplius, and because it exhibits morphological characteristics of other closely related cyclopoid nauplii.

Hemicyclops adhaerens (Wilson, 1932a, spelled it *adherens*) was first described by Williams (1907). He found the adult to be benthonic and present records indicate that the nauplius is free-swimming with descent to the bottom apparently taking place in early copepodid instars. Gooding (1960) has redescribed the female from Narragansett Bay and indicated that *H. americanus* Wilson (1932b) from Chesapeake Bay is synonymous.

Several illustrations showing details of its body shape and appendages appear justified here since no nauplii of any species of *Hemicyclops* has been described. Figures 32 and 33 show ventral views of two different instars and Fig. 31 shows a lateral view of the oldest instar. Development is typically anamorphic with all the appendages quite normal. The elliptical body and short symmetrical pair of caudal spines are characteristic of many other cyclopoid nauplii. A prominent long spine attached to each antenna extends posteriorly to the opposite first maxilla (note arrow in Fig. 32). This pair of spines appears as a large X when the nauplius is viewed ventrally, a diagnostic feature evident on all nauplii examined. The number of naupliar instars of this species is not known.

The caudal armature has a medial pair of short spines in all the instars. In addition there are two pairs of setae lateral to these spines. On the early-

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[5] Obtained from Dr Perry H. Jeffries, Narragansett Marine Laboratory, University of Rhode Island. Sample taken on July 18, 1960.

[6] Identified by Dr Richard V. Gooding, Department of Biology, Boston University.

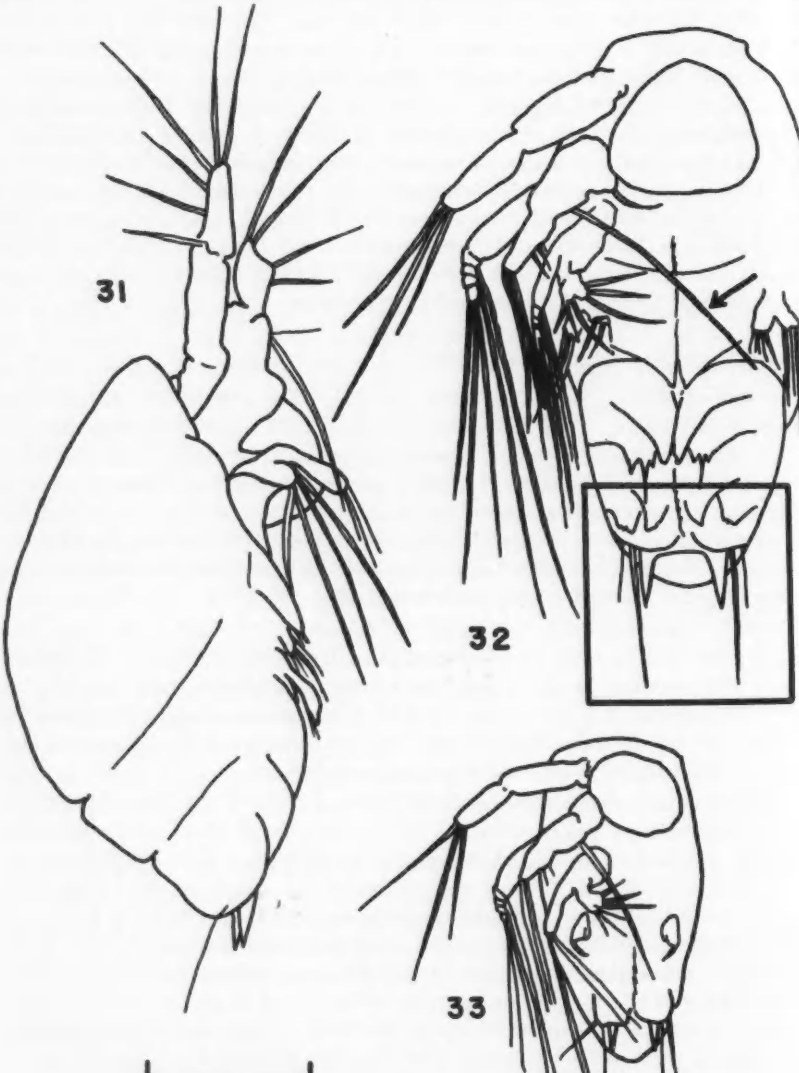

FIG. 31–33. Nauplii of *Hemicyclops adhaerens* (Williams). Figures drawn from West Passage specimens. **31**. Right side of oldest nauplius. **32**. Ventral view of oldest nauplius. Arrow points to prominent spine on antenna. Enclosed area shows a view of the caudal armature considered in key. **33**. Ventral view of early-stage.

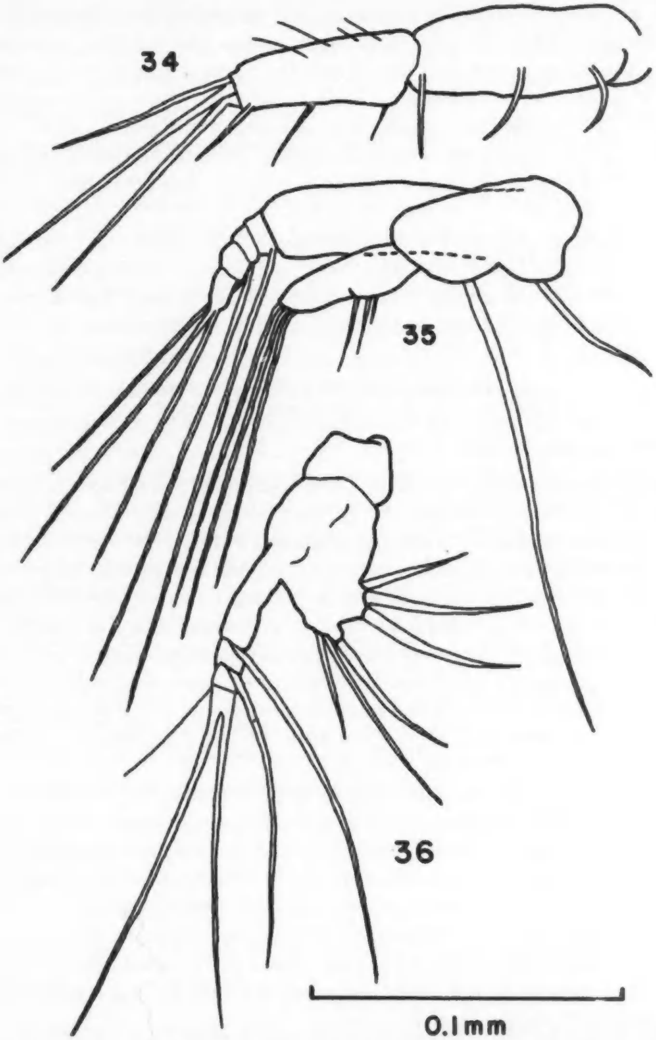

FIG. 34–36. Appendages of the nauplius of *Hemicyclops adhaerens* (Williams). **34.** Ventral view of right antennule. **35.** Ventral view of right antenna. **36.** Ventral view of right mandible.

stage nauplius (Fig. 33) the shorter outer pair of setae is stouter than the inner pair but the inner pair appear stouter on the oldest nauplius (Fig. 32).

The antennule (Fig. 34) has two long segments and possibly another short one at its proximal end. Three setae terminate the distal segment. Several short setae and spines are scattered along the antennule.

The antenna (Fig. 35) is biramous, the exopodite five-segmented and the endopodite unisegmented. The basal segment has two masticatory spines. The longest is the spine mentioned previously that appears with its counterpart as a large X when the nauplius is viewed ventrally. Three setae terminate the endopodite while three short spines originate about midway along it. Two setae terminate the distal segment of the exopodite. Three other setae arise from the ends of segments, one from the end of the fourth, one from the third, and another from the first.

The mandible (Fig. 36) is also biramous, the exopodite four-segmented and the endopodite fused with the basal segment. Two setae terminate the exopodite with a third arising from the end of the second and a fourth from the first. The endopodite has two groups of three stout spines.

KEY TO THE COMMON FREE-SWIMMING COPEPOD NAUPLII OF NARRAGANSETT BAY

USE OF KEY

This key separates the nauplii of those species listed in Table I. Two species that were not collected during the present study were included in the key because they are known from nearby estuarine waters. The key is based exclusively on caudal armatures and is entirely artificial. Since each of the 16 species has up to six naupliar instars, each with a distinctive arrangement of the caudal armature, it would be a formidable task to construct a key to all 96 instars, hence only an early and late-stage instar have been keyed. The caudal armature of Nauplius VI is keyed for all the free-swimming copepods and the oldest one (presumably Nauplius V) for *Hemicyclops adhaerens* and *Longipedia helgolandica*; also an early-stage instar (usually Nauplius III but sometimes Nauplius II or IV) is keyed.

With a little experience in keying nauplii, the sizes of the different instars can be useful in confirming an identification. The average size of an instar was found to be meaningless as a key character, for there were measurable variations in size during the year, but variations of size in individual samples were usually small enough so that one instar was distinguishable from another. The differences in size between species were also useful.

Figure 32 illustrates with an enclosure the ventrocaudal view of the caudal armature of *Hemicyclops adhaerens* and it is this view that is considered in the key and illustrated in the figures.

1a. Caudal armature elements arranged asymmetrically; stoutest and longest element arising from either right or left side 2

1b. Caudal armature elements arranged symmetrically; stoutest but not necessarily the longest element, either paired or single 13

2a(1a). Stoutest spine on right side 3

2b. Stoutest spine on left side 8

3a(2a). Prominent spine not plumose 4

3b. Prominent spine plumose .... *P. coronatus*. 7

4a(3a). More than 2 caudal armature elements.................................. 5

4b. Two caudal armature elements................(Fig. 15), early-stage *T. discaudatus*

5a(4a). Dorsally curved spine on left side..............(Fig. 16), late-stage *T. discaudatus*

5b. Ventrally curved spine on left side..........................*T. setacaudatus.* 6

6a(5b). Five caudal armature elements; a tuft of hair on distal end of ventrally curved spine....................................(Fig. 30), late-stage *T. setacaudatus*

6b. Less than 5 caudal armature elements.........(Fig. 29), early-stage *T. setacaudatus*

7a(3b). Four caudal armature elements, 2 arising from each side...(Fig. 28), late-stage *P. coronatus*

7b. Two or 3 caudal armature elements.............(Fig. 27), early-stage *P. coronatus*

8a(2b). Prominent spine on right side... 9

8b. Prominent spine on left side... 11

9a(8a). Prominent spine on left side with gradual taper from base to tip.............. 10

9b. Prominent spine on left side with medial bulge on proximal one-third...(Fig. 18), late-stage *E. herdmani*

10a(9a). Four caudal armature elements, 2 lateral spines and 2 medial setae...(Fig. 8), late-stage *T. longicornis*

10b. Less than 4 caudal armature elements...........(Fig. 17), early-stage *E. herdmani*

11a(8b). Left side with a seta that is at least three-quarters length of prominent spine; a large nauplius................................(Fig. 20), late-stage *L. aestiva*

11b. Not as in 11a... 12

12a(11a). One or 2 setae medial to spines.................(Fig. 7), early-stage *T. longicornis*

12b. Not as in 12a.................................(Fig. 19), early-stage *L. aestiva*

13a(1b). Caudal armature spines paired.. 14

13b. Caudal armature dominated by a medial, unpaired spine................... 28

14a(13a). Caudal armature with normal spines and/or setae........................ 15

14b. Caudal armature dominated by numerous short, stubby spines one of whose edges is usually uneven; a single pair of crossed setae at extreme caudal end...*P. minutus* 24

15a(14a). Prominent pair of spines not plumose.................................. 16

15b. Prominent pair of plumose spines; caudal armature may show slight asymmetry ....*E. hirundoides.* 25

16a(15a). Prominent pair of spines with slender bases one-quarter or less their length.... 17

16b. Prominent pair of spines with broad bases one-half to one-third their length.. 26

17a(16a). Two pairs of setae arising ventrally and directed at about 30° angle from midline ....(Fig. 3), early-stage *O. similis*

17b. Not as in 17a... 18

18a(17b). Pair of curved spines arising from extreme caudal end of cylindrical abdomen ....(Fig. 25), early-stage *P. crassirostris*

18b. Not as in 18a... 19

19a(18b). Pair of setae arising medial to prominent pair of spines..................... 20

19b. Pair of setae arising lateral to prominent pair of spines.................... 22

20a(19a). Two pairs of spines with longer pair of crossed setae.................... 21

20b. Pair of spines with longer pair of crossed setae. The morphological characteristics of these 2 early-stage nauplii are very similar and their identifications are best confirmed by the seasonal appearance of late-stage nauplii.................. ....(Fig. 11 and 13), early-stage *A. clausi* and *A. tonsa*

21a(20a). Two pairs of spines about equal in length; tips of most posterior pair usually touching and creating an angle of about 90°..........(Fig. 14), late-stage *A. tonsa*

21b. Two pairs of spines unequal in length; spines parallel or nearly so............ ....(Fig. 12), late-stage *A. clausi*

22a(19b). Lateral pairs of setae slightly shorter than prominent pair of spines........... 23

22b. Lateral pairs of setae longer than prominent pair of spines.................. ....(Fig. 23), early-stage *O. brevicornis*

23a(22a). Lateral pairs of setae showing some taper, spine-like....(Fig. 4), late-stage *O. similis*

23b. Slender lateral pairs of setae...................(Fig. 24), late-stage *O. brevicornis*

24a(14b). More than 6 caudal armature elements.............(Fig. 6), late-stage *P. minutus*

24b. Six or less caudal armature elements...............(Fig. 5), early-stage *P. minutus*

25a(15b). Embryonic buds of swimming legs present.......(Fig. 10), late-stage *E. hirundoides*

25b. Pair of plumose spines arising ventrally and directed toward caudal armature; no embryonic buds of swimming legs...........(Fig. 9), early-stage *E. hirundoides*

26a(16b). Some elements 2 or 3 times as long as prominent pair of spines....*H. adhaerens.* 27

26b. All elements same length or shorter than prominent pair of spines........... ....(Fig. 26), late-stage *P. crassirostris*

27a(26a). Pair of setae longer and pair of setae as long as pair of spines............... ....(Fig. 32), late-stage *H. adhaerens*

27b. Two pairs of setae longer than pair of spines.....(Fig. 33), early-stage *H. adhaerens*

28a(13b). Dorsally directed seta almost as long as medial unpaired spine; caudal armature slightly asymmetrical......................................*C. hamatus.* 29

28b. No dorsally directed seta; caudal armature truly symmetrical....*L. helgolandica.* 30

29a(28a). Two pairs of spines arising ventrally................(Fig. 2), late-stage *C. hamatus*

29b. Single pair of spines arising ventrally.............(Fig. 1), early-stage *C. hamatus*

30a(28b). Medial, unpaired spine about one-fifth length of body; pair of nonplumose spines lateral to medial spine........................(Fig. 22), late-stage *L. helgolandica*

30b. Medial, unpaired spine about one-half or more length of body; pair of plumose spines lateral to medial spine................(Fig. 21), early-stage *L. helgolandica*

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Lecithinase Activity in the Muscle of Rainbow Trout (*Salmo gairdnerii*)[1]

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ABSTRACT

A radioactive tracer procedure for determination of the various lecithin hydrolysing enzymes, at a low level of activity, is described. The procedure involves the use of phospholipids labeled with C^{14} in the choline moiety as substrate and the measurement of radioactivity released in the various products of hydrolysis. The pathway of lecithin catabolism in trout muscle is via glycerylphosphorylcholine. Of the other possible routes of breakdown of lecithin, there was no indication for the activity of phospholipase C or D. Greater enzymic activity was present in the lateral line muscle than in the white muscle. The enzyme which is responsible for hydrolysis of lecithin to glycerylphosphorylcholine showed optimum activity in the vicinity of *p*H 7 did not require Ca^{++} for activity and was partially inhibited by Hg^{++}. A lysolecithinase, showing similar properties, but having a comparatively greater activity, was also present in trout muscle.

INTRODUCTION

Although phospholipid hydrolysis is known to occur in fish muscle (Cardin et al., 1958; Lovern et al., 1959; Olley and Lovern, 1960; Bligh, 1961; Yurkowski and Brockerhoff, 1965), the sequence of the enzymic reactions involved is not fully known. In other animals, the different pathways of phospholipid hydrolysis have not been investigated in the muscular tissue and the presence of a lecithinase was demonstrated only recently in mammalian skeletal muscle (Gallai-Hatchard and Thompson, 1965). As muscle appears to be one of the animal tissues with very low phospholipase activity, an assay procedure was developed which allows measurements of lower levels of enzymic activity than that possible by conventional methods. The procedure involved the use of phospholipids labelled with C^{14} in the choline moiety as substrate and the measurement of radioactivity released in the various products of hydrolysis. By means of this procedure the occurrence in trout muscle of different pathways of lecithin hydrolysis has been investigated. In order to account for all the enzymic activity in the muscle, tissue slices or homogenates, rather than extracts, were employed.

MATERIALS AND METHODS

Chemicals

A sample of glycerylphosphorylcholine was kindly supplied by Dr Morris Kates, National Research Council, Ottawa. Choline-methyl C^{14} chloride was

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obtained from New England Nuclear Corporation, Boston, Mass. The other chemicals were commercial samples of the purest grade available. Venom from eastern diamondback rattlesnake (*Crotalus adamanteus*) was obtained from Sigma, St. Louis, Mo.

FISH

Rainbow trout (*Salmo gairdnerii*) about 2 years old, weighing 200–300 g, were obtained from a commercial hatchery. They were fed with New Age complete trout fingerling pellets (J. R. Clark Co., Salt Lake City, Utah). The fish used had not been fed for about 20 hr prior to killing.

ANALYTICAL METHODS

Total phosphorus was determined by the method of King (1932). Choline was estimated according to the procedure of Glick (1944) and total nitrogen by a microkjeldahl method (Steyermark, 1951).

PAPER CHROMATOGRAPHY

Chromatography, one-directional ascending, using Whatman No. 1 filter paper, was employed. The following solvent systems were used: ethanol–concentrated ammonia–water (EAW), 90:5:5, v/v (Bregoff et al., 1953); *n*-propanol–concentrated ammonia–water (PAW), 6:3:1, v/v (Dawson, 1955); *n*-butanol–acetic acid–water (BAcW), 5:3:1, v/v (Kates, 1954, 1960); *n*-propanol–acetic acid–water (PAcW), 8:1:1, (Huennekens et al., 1954). Compounds were identified by their R_F values compared to those of standards. The modified Dragendorff reagent (Bilinski, 1964) and 0.2% ninhydrin in 95% ethanol (Block et al., 1952) were used for developing the chromatograms. The distribution of radioactivity in various R_F zones was determined after elution with 80% methanol using the reineckate precipitation procedure (see Measurement of Radioactivity).

PREPARATION OF C^{14} LABELLED SUBSTRATES

Phospholipids were labelled *in vivo* with C^{14} in the choline moiety. Choline-methyl-C^{14} chloride was administered intraperitoneally to rainbow trout in a single dose (approximately 10 μc and 3 μmoles per 100 g body weight). The fish were anaesthetized with 2-phenoxyethanol (Sehdev et al., 1963) during the injection. They were killed after 15–20 hr. Total lipid extracts were prepared from the combined liver, kidney, and blood by the method of Folch et al. (1957). In order to obtain a lipid extract free from contamination by the free choline C^{14} used for injection, the crude extract was subjected to five extractions with "pure solvent upper phase" containing 0.02% $CaCl_2$ as described by Folch et al. (1957). In a preliminary fractionation, neutral lipids were removed by elution with chloroform from silicic acid, followed by the elution of phospholipids with methanol (Borgstrom, 1952).

Phospholipid labelled with choline-methyl-C^{14} (PL-C^{14}) used as substrate for determination of lecithinase activity, was obtained free from lysolecithin and sphingomyelin by silicic acid chromatography using chloroform–methanol (3:2, v/v) as eluent (Hanahan et al., 1957; Robertson and Lands, 1962). PL-C^{14} had the following composition: P 3.60–3.80%; N 1.70–1.90%; choline 9.0–9.5%. The total radioactivity in choline expressed as counts per minute per milligram (cpm/mg) phospholipid was 25,000–35,000. Phospholipid isolated from trout muscle by the same procedure had approximately one-fifth the specific activity. Lysophospholipid labeled with choline-methyl C^{14} (LyPL-C^{14}), used as substrate for determination of lysolecithinase activity, was prepared by action of snake venom (*Crotalus adamanteus*) on phospholipid-C^{14}, followed by isolation of lysolecithin by silicic acid chromatography, according to the procedure of Hanahan et al. (1960). LyPL-C^{14} contained 20.0–21.0% choline and the total radioactivity in choline was approximately 70,000 cpm/mg LyPL-C^{14}.

Mixed phospholipids labeled with choline, rather than a pure preparation of lecithin were used as substrate, because it was expected that the lecithinases might have a low level of activity in fish muscle and it is known that the hydrolysis of pure lecithin could be very effectively activated by the presence of other phospholipids (Dawson, 1958). Since a procedure specific for the determination of radioactivity in choline was used (see Measurement of Radioactivity), the presence in the substrate of phosphatidyl ethanolamine or of other phospholipids containing no choline would not interfere with the determination of lecithinase or lysolecithinase activity.

TISSUE PREPARATIONS

Fish were stunned, killed by decapitation, and tissue slices were prepared as previously described (Bilinski, 1963). For preparation of homogenates, freshly obtained slices were cut into small pieces with scissors, suspended in buffer solution, and homogenized for 1 min in a Potter-Elvehjem homogenizer. All the operations were carried out at 0–3 C.

INCUBATION PROCEDURE

Incubation was conducted in a constant temperature bath provided with a shaking device. The total volume of the medium was 5.0 ml. Unless otherwise stated, the reaction mixture was composed of 150 μmoles Na-K phosphate buffer, *p*H 6.5; 500 mg tissue; 5 mg PL-C^{14} or 1.25 mg LyPL-C^{14}. The incubation period was 120 min at 35 C. At the end of the incubation the reaction mixture was rapidly cooled in an ice bath and 0.75 ml of 5% of serum albumin was added to assist in precipitation of lysolecithin (Shapiro, 1953; Dawson, 1956). The mixture was treated with 3.0 ml 10% (w/v) trichloracetic acid, centrifuged and filtered in the cold. The precipitate obtained was washed twice with 3.0 ml 5% (w/v) trichloracetic acid. When PL-C^{14} served as substrate, the filtrate was extracted five times with 0.5 vol diethylether in order to free the aqueous solution from contamination by C^{14} phospholipids. With

LyPL-C^{14} as substrate, the filtrate was extracted once with 3 vol of chloroform–isobutanol (2:1, v/v) mixture (Chatterjee and Mitra, 1962). Aliquots of the aqueous phase were taken for the subsequent determinations. For the determination of the *p*H–activity curve, incubation was conducted in buffers at a final concentration of 0.1 M. The following buffers were used: Na acetate–acetic acid at *p*H 4.0, 5.0, and 5.5; KH_2PO_4–Na_2HPO_4 at *p*H 6.0, 7.0, and 8.0, and borate–KCl at *p*H 8.0, 9.0, and 10.0. Final *p*H adjustments if necessary were made after addition of the tissue to buffer solution.

ESTIMATION OF THE PRODUCTS OF HYDROLYSIS

This was accomplished by measurement of the radioactivity in free and bound choline, released by hydrolysis of the C^{14} labeled substrates. The following procedures were used in order to distinguish between the various choline-containing products of hydrolysis.

A. *Free choline.* Radioactivity in choline isolated as the reineckate from the aqueous phase after incubation.

B. *Glycerylphosphorylcholine* (GPC). Increase in radioactivity in choline over that found in A, after hydrolysis of the aqueous phase in 1 N HCl at 100 C for 20 min. Under these conditions GPC is quantitatively hydrolysed to choline, whereas phosphoryl choline is not attacked to any appreciable extent (Schmidt, 1957).

C. *Phosphoryl choline.* Increase in radioactivity in choline over that found in B after hydrolysis of the aqueous phase in 2 N HCl at 125 C for 5 hr in sealed tubes. By this treatment, in addition to GPC, phosphorylcholine is hydrolysed with liberation of choline. Under the conditions of hydrolysis employed a cleavage of approximately 50% of phosphorylcholine is obtained (Baer and McArthur, 1944).

D. *Lysolecithin.* When the formation of lysolecithin was to be determined the incubation was conducted as described above. The reaction was stopped by addition of 5 ml 80% methanol in chloroform and the isolation of lysolecithin from the incubation mixture was carried out essentially as described by Robertson and Lands (1962) using silicic acid chromatography. Prior to the determination of radioactivity, the lysolecithin fraction was subjected to chemical hydrolysis to release choline (Glick, 1944).

MEASUREMENT OF RADIOACTIVITY

For the determination of radioactivity in choline the procedure described by Tolbert and Okey (1952) was employed with a few modifications. To an aliquot of the solution containing free choline 350 μg carrier choline was added. The volume was made up to 5.0 ml after adjusting the *p*H to the turning point of phenolphthalein and an equal volume of saturated aqueous solution of ammonium reineckate was added. After standing overnight at 1–4 C the precipitate was collected by filtration on discs of Whatman filter paper No. 3 (plated area 3.8 cm^2) and washed with *n*-propanol. The discs were counted, using a Nuclear Chicago gas flow counter, provided with a Micromill window. Substrate blanks, made by conducting the incubation in absence of tissue, amounted to less than 0.1% of the total radioactivity when PL-C^{14} served as substrate. Comparatively higher although constant blanks, amounting to not more than 0.4%, were obtained when LyPLC^{14} was employed as substrate.

The total radioactivity in choline present in PL-C^{14} or LyPL-C^{14} used as substrate was determined by reineckate plating, after a complete chemical hydrolysis, achieved by heating for 90 min on a steam bath in 3 N $Ba(OH)_2$ (Glick, 1944).

The method used for calculating the results is as described previously (Bilinski, 1963). The specific activity is expressed as millimicromoles choline released per gram wet tissue per hour.

In preliminary experiments the conditions for the quantitative measurement of radioactivity in choline, plated as choline reineckate, were investigated. The effect of choline concentration on the recovery of radioactivity in choline reineckate is shown in Fig. 1. At very low choline concentrations, the counting rate was below its maximum due to an incomplete precipitation of choline. At high choline concentrations a decrease in counting rate also occurred due to the self-absorption effect. Under the experimental conditions used (plating

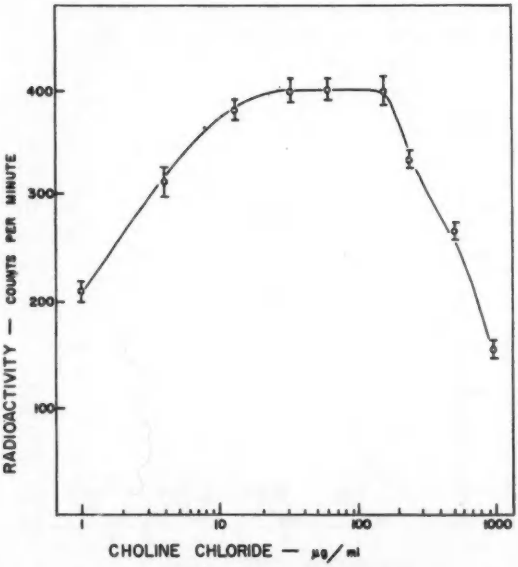

FIG. 1. Effect of choline concentration on the measurement of radioactivity by plating as choline reineckate. Note: Constant amount of choline-methyl-C^{14}, final volume 10 ml, plated area 3.8 cm^2. Each point represents the mean value from four experiments, the standard deviations are indicated by a vertical line.

area 3.8 cm^2, total volume of solution 10 ml) at a concentration of 30–150 μg/ml a maximum counting rate independent of choline concentration was obtained. This range of choline concentration was used in the procedure adopted by adding carrier choline to the comparatively small amounts of radioactive choline liberated in the product of hydrolysis.

Experiments were also conducted to establish that the reineckate precipitation is a procedure specific for determination of radioactivity in choline. An aliquot of PL-C^{14} was subjected to a complete chemical hydrolysis and the material giving a precipitate with ammonium reineckate collected. After being separated from reineckate (Arnstein, 1960) it was subjected to paper chromatography. With the two solvent systems used (EAW and BAcW) it was found that all the radioactivity present was located at R_F zones corresponding to the standard choline only. By developing paper chromatograms with the Dragendorff reagent and ninhydrin it was confirmed that choline was the only detectable compound obtained by the reineckate precipitation.

RESULTS

The experiments reported in Fig. 2 were aimed at identifying the lecithin hydrolysing enzymes active in the lateral line muscle. The various water-soluble

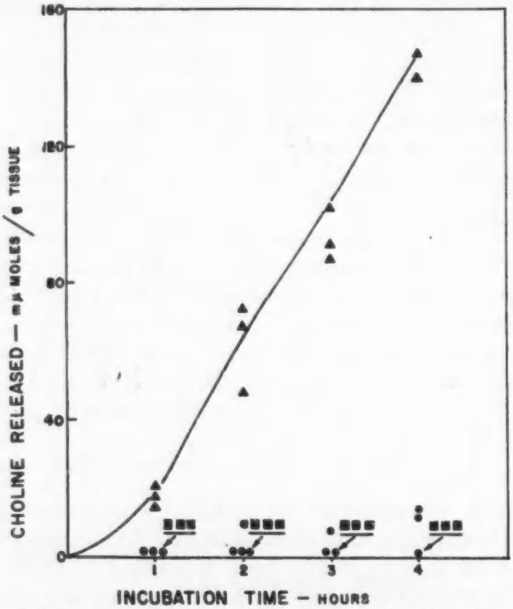

FIG. 2. Effect of time of incubation on lecithinase activity in tissue slices from lateral line muscle. Products of hydrolysis: ● free choline, ■ phosphorylcholine, ▲ glycerylphosphorylcholine. Unless otherwise stated the standard conditions of assay were employed (see Materials and Methods).

products of hydrolysis, containing choline, were estimated after an incubation period of 1–4 hr. As shown in the figure, there was no formation of phosphorylcholine, and free choline was also absent or present in trace amounts only. The main product of hydrolysis was in the form of bound choline, labile to mild and hydrolysis, indicating the presence of GPC. The liberation of GPC showed a linear increase with duration of incubation. Paper chromatography was used to identify GPC. In the four solvent systems used (EAW, PAW, BAcW, PAcW) over 85% of the radioactivity was found at the R_F zone corresponding to standard GPC. In subsequent experiments some of the properties of the lecithinase(s) responsible for liberation of GPC were investigated. The optimum temperature for the enzymic activity during an incubation of 2 hr was determined. As shown in Fig. 3 the maximum activity was found between 35 and 45 C with a sharp decrease at 50 C. At 25 C only a very limited activity could be observed. The inactivation of the enzyme by heat was also determined. As indicated in Table I, heat treatment at 100 C suppressed all the activity, whereas heating at 70 or 60 C resulted in an approximately 90% inactivation. The effect of various additives on lecithinase activity is shown in Table II. The addition of Ca^{++} had no effect on the activity. The activity was only slightly impaired by addition of ethylenediamine tetracetate (EDTA), but Hg^{++} ions had a considerable inhibitory effect at the concentration used. A series of buffers with

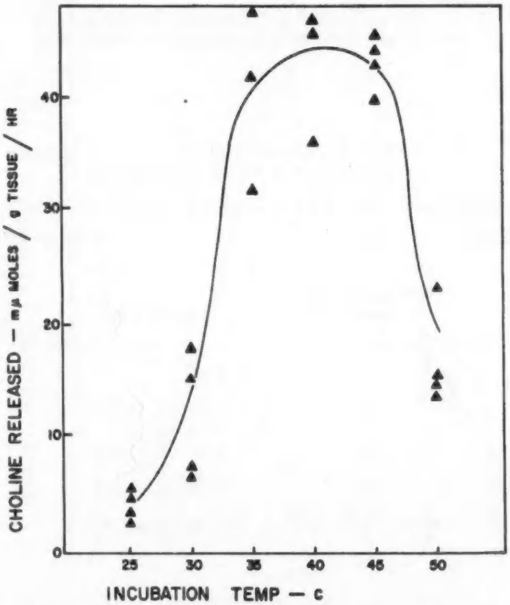

FIG. 3. Effect of temperature on lecithinase activity in tissue slices from lateral line muscle. (Symbols explained in Fig. 2.)

TABLE I. Heat inactivation of lecithinase in tissue slices from lateral line muscle of rainbow trout.

Heat treatment at *p*H 6.5		Lecithinase
Temp (*C*)	Duration (*min*)	Relative activity[a]
–	–	1.00
100	30	nil
100	10	nil
70	30	0.07 ± 0.02 (4)[b]
70	10	0.09 ± 0.01 (4)
60	30	0.08 ± 0.01 (4)
60	10	0.10 ± 0.02 (4)

[a] Formation of GPC in comparison with experiments run with the same preparation which has not been subjected to heat treatment. The standard conditions of assay were employed (see Materials and Methods).

[b] Mean value and standard deviation. The number of experiments is indicated in parentheses.

TABLE II. Effect of various additives on the lecithinase and lysolecithinase activity in rainbow trout lateral line muscle homogenates.

Additive		Relative activity[a]	
Compound	Concentration (mM)	Lecithinase	Lysolecithinase
No addition	–	1.00	1.00
$CaCl_2$	1	0.98 ± 0.14(4)[b]	0.92 ± 0.05(4)[b]
$CaCl_2$	10	1.00 ± 0.07(4)	–
EDTA	2	0.88 ± 0.19(4)	0.98 ± 0.04(4)
$HgCl_2$	1	0.36 ± 0.20(4)	0.09 ± 0.01(4)
Na desoxycholate	5	–	0.21 ± 0.03(4)

[a] Formation of GPC in comparison with experiments run with the same preparation under standard conditions of assay (see Materials and Methods).

[b] Mean value and standard deviation. The number of experiments is indicated in parentheses.

*p*H values between 4 and 10 were used to determine the optimum *p*H for lecithinase activity. As shown in Fig. 4 the maximum activity was in the vicinity of *p*H 7, although there was a considerable activity between *p*H 6 and 8. A further lowering of *p*H resulted in a sharp decrease of activity. The changes of *p*H had no noticeable effect on the liberation of free choline, which was either absent or present in trace amounts only at the wide range of *p*H tested. As shown in Fig. 5, the rate of the reaction increases with the tissue concentration, but an increase in the amount of tissue over a concentration of 10% did not result in a further increase of the activity. The experiments described were conducted at constant substrate concentration of 1 mg/ml. There was no decrease in the activity when this amount was decreased to 0.5 mg/ml. Sonification of the substrate did not result in a well-marked increase of enzymic activity. As shown in Table III, lecithin hydrolysis with formation of GPC occurs also in the white dorsal muscle but the enzymic activity is lower than in the lateral line muscle.

In another series of experiments, the formation of lysolecithin as a product of hydrolysis was determined by silicic acid chromatography. It was found with lateral line muscle that after 2–4 hr of incubation, there was no formation of detectable amounts of lysolecithin. Addition to the standard incubation

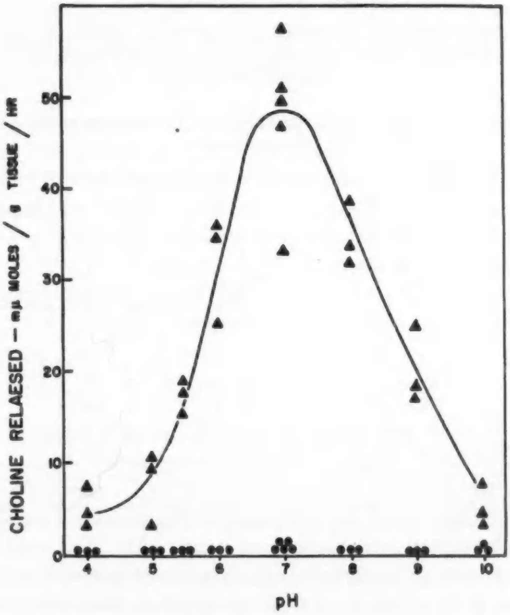

FIG. 4. Effect of *p*H on lecithinase activity in lateral line muscle homogenates. Incubation was conducted in 0.1 M buffers. For composition of buffer solutions see Materials and Methods. (Symbols explained in Fig. 2.)

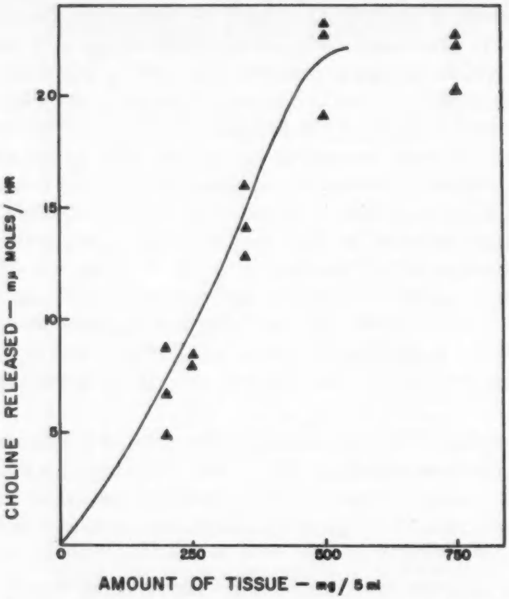

FIG. 5. Effect of the amount of tissue on lecithinase activity in tissue slices from lateral line muscle. (Symbols explained in Fig. 2.)

TABLE III. Lecithinase and lysolecithinase activity in rainbow trout white dorsal muscle homogenates.

	Incubation temp[a] (*C*)	Products of hydrolysis		
		Free choline	GPC (*mμ moles/g tissue/hr*)	Phosphoryl choline
Lecithinase	35	Nil	6 ± 2(7)[b]	Nil
Lecithinase	40	Nil	11 ± 2(7)	–
Lysolecithinase	35	Nil	152 ± 16(8)	–

[a] The standard conditions of assay were employed (see Materials and Methods).
[b] Mean value and standard deviation. The number of experiments is indicated in parentheses.

mixture of desoxycholate which is known to inhibit lysolecithinase (Magee et al., 1962) did not result in accumulation of lysolecithin. However, under the conditions used, the lysolecithinase activity was not inhibited completely (see below).

The presence of lysolecithinase in trout muscle was also investigated. As shown in Fig. 6, in the lateral line muscle the activity of lysolecithinase is

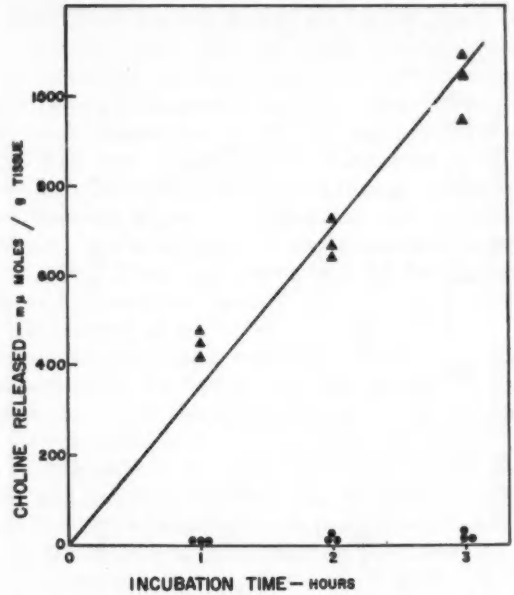

FIG. 6. Effect of incubation time on lysolecithinase activity in tissue slices from lateral line muscle. (Symbols explained in Fig. 2.)

comparatively higher than that of lecithinase. The hydrolysis of lysolecithin is associated with the release of GPC and with no formation of free choline. As indicated in Fig. 7, the enzyme has also an optimum activity at the vicinity of *p*H 7. The effect of various additives on the activity is shown in Table II. The addition of Ca^{++} and EDTA had no effect on the activity. The enzyme was almost completely inhibited by Hg^{++} ion, but still showed some activity in presence of desoxycholate. As shown in Table III, lysolecithinase is present in the white dorsal muscle and has a much higher activity than the lecithinase.

DISCUSSION

The pathway of lecithin catabolism in trout muscle is via GPC. Of the other known routes of breakdown of lecithin, there is no indication for the activity of phospholipase C or D, which would result in formation of free choline and phosphorylcholine, respectively. Regarding the enzyme(s) responsible for the formation of GPC, both lecithinase and lysolecithinase activities were demonstrated. In view of the activity of lysolecithinase, there is no indication whether the lecithinase present in the trout muscle liberates one or both fatty acids from the lecithin molecule. The accumulation of GPC as the end product of hydrolysis would suggest that the glycerylphosphorylcholine diesterase had no activity under the conditions suitable for lecithin hydrolysis. The

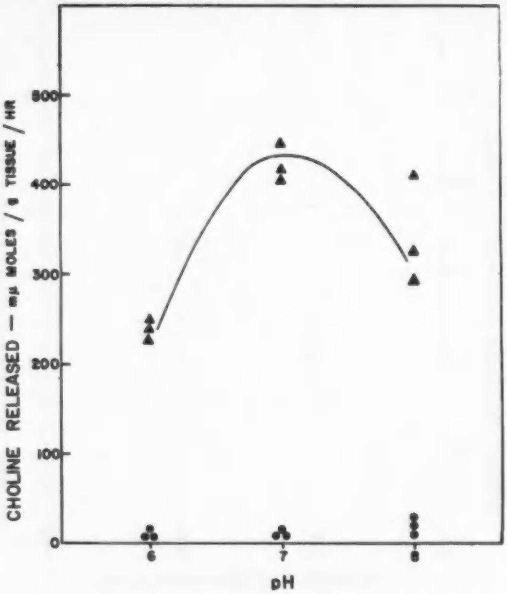

FIG. 7. Effect of *p*H on lysolecithinase activity in lateral line muscle homogenates. Incubation was conducted in 0.1 M phosphate buffers. (Symbols explained in Fig. 2.)

higher enzymic activity found in the lateral line than in the dorsal muscle is consistent with presence of larger amounts of phospholipids in this tissue (Love et al., 1959).

In mammals, skeletal muscle is one of the tissues with the lowest activity of phospholipid splitting enzymes. The presence of lysolecithinase in rat skeletal muscle was demonstrated by Marples and Thompson (1960) and only very recently Gallai-Hatchard and Thompson (1965) have shown that lecithin is hydrolysed with formation of free fatty acids by preparations from rat skeletal muscle. These appear to be the only reports demonstrating the presence of phospholipases in the mammalian skeletal muscle. It is known that in various other mammalian tissues lecithin hydrolysis can result in formation of GPC without the accumulation of lysolecithin as intermediate (for review see Kates, 1960a, see also Robertson and Lands, 1962). In view of the recent demonstration that phospholipase A is widely distributed in mammalian tissues (Van Den Bosch and Van Deenen, 1964; Rossi et al., 1964, 1965; Gallai-Hatchard and Thompson, 1965) it seems very probable that GPC is formed by the action of phospholipase A followed by that of lysolecithinase, rather than under the action of a single enzyme.

The autolytic hydrolysis of phospholipid in fish flesh is known to take place during cold storage and processing of fish and it has been investigated extensively in this connection (for review, see Lovern, 1962; Lovern and Olley, 1962; Dyer and Dingle, 1961). Although these investigations were conducted with different species of fish and the overall hydrolytic cleavage during storage, rather than the presence of specific enzymes, was determined, the observed course of hydrolysis is consistent with the enzymic activity found to be present in trout muscle. The most detailed studies have been made with cod and it was shown that in phospholipid hydrolysis during cold storage of cod flesh fatty acids are liberated with a corresponding loss of lipid phosphorus and lysophosphatides do not accumulate to any detectable extent (Lovern et al., 1959; Olley et al., 1962). There was also no evidence for the activity of phospholipase C or D, as indicated by the lack of accumulation of diglycerides and phosphatidic acid (Lovern et al., 1959).

Since our investigation was completed, a study on lysolecithinase of cod muscle was published by Yurkowski and Brockerhoff (1965). The results of this investigation show that the lysolecithinase of cod muscle is similar in its properties to the lysolecithinases of mammalian tissues and to that found by us in rainbow trout muscle. Lysolecithin was hydrolysed to free fatty acid and GPC and oleic acid strongly inhibited this reaction. Although the study of Yurkowski and Brockerhoff deals with the properties of lysolecithinase only, it is indicated that a low level of lecithinase activity could be demonstrated in fresh extracts from cod muscle.

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Dynamics and Exploitation of Lake Whitefish in Southern Georgian Bay[1,2]

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ABSTRACT

Instability of the population of *Coregonus clupeaformis* (Mitchill) in southern Georgian Bay from 1948 to 1964 was evidently partly due to intensive fishing.

The population was discrete at least from 1956 to 1964 as determined by extensive tagging. From 1948 to 1964, estimated effective fishing effort varied 10-fold and annual yields almost 20-fold, with two cycles of abundance and scarcity. Strength of 1951–59 year-classes, defined as population size at age III, varied 40-fold. In spite of the marked instability, the population was in recent years more stable than any other whitefish population in Georgian Bay or Lake Huron.

Almost all the commercial catch was made with gill nets of 4½-inch mesh. In 1957, fishing depended largely on age VII–IX fish; by 1964, on those of age V and VI. Apparent growth rate increased during this period: in 1957 age XII fish weighed 3.4 lb; in 1964 age VI weighed 3.7 lb. From 1959 to 1964, reproduction depended largely on males age IV+ and older and longer than 17 inches, and on females age V+ and older and longer than 18 inches.

Natural mortality coefficients (exponential model) averaged 0.41 for fish of the 1948–58 year-classes beyond age III. Gillnetting was largely restricted to 2 months in late spring and two in fall. In each fishing season these gill nets took about 40% of the survivors of a year-class after it became fully vulnerable, at ages V, VI, and VII during the early 1960s.

Combining growth and natural mortality rates in a biomass curve indicated that individual year-classes would provide highest yields when fished intensively at age IV, or slightly earlier than they were fished in the early 1960s. Yet the only hypothesis that might explain the continued existence of a fishable population was that relatively large parts of the habitat were either legally closed or unsuitable for fishing. Evidently the fishing was intense and increasing the effort would mean risk of a population collapse.

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INTRODUCTION

OUR OBJECTIVES in this study were to describe, as fully as our data permitted, the life history and dynamics of lake whitefish in southern Georgian Bay; to describe the fishery; and to measure the effect of the fishery on the population. The lake whitefish, *Coregonus clupeaformis* (Mitchill), has been a preferred commercial species in the Great Lakes for well over a century. In some decades it was the most preferred fish; in others it yielded its favored position to the lake trout,[4] the lake herring, or the walleye. In 1965 all four species were at low levels of abundance in the four lower lakes.

There have been numerous studies on whitefish in the Great Lakes, e.g. Hart (1931), Smith and Van Oosten (1939), Van Oosten (1939), Doan (1942), Budd (1957), Edsall (1960), Budd and Cucin (1962), and Christie (1963). Findings differ from lake to lake and from population to population. Tagging studies indicate that individual lakes generally contain a number of populations, which may overlap geographically for parts of the year at least. Some populations are more migratory than others. Growth rates and age at sexual maturity may differ markedly from one lake to the next. Natural and fishing mortality rates have not been reported for these lakes.

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[4] Common names of fish are those recommended in the American Fisheries Society Special Publication No. 2, 1960, except that "whitefish" is used for "lake whitefish" and "lamprey" for "sea lamprey."

Recent annual production of lake whitefish from the Great Lakes has either been much below that of two or three decades past or has fluctuated more markedly from year to year (Baldwin and Saalfeld, 1962). The declines and instability of the populations have been ascribed by different authors to one or more of the following factors: pollution of spawning grounds, gradual eutrophication, changing climate, lamprey predation, smelt predation, and overfishing.

SOUTHERN GEORGIAN BAY

The study area was Georgian Bay District IV (Fig. 1, 2).

Ordovician shales underlie most of southern Georgian Bay. The northeastern shore with its thirty thousand islands is composed of hard Precambrian rock.

The main tributaries drain agricultural land. Water in the bay is quite hard with total dissolved solids of 100–165 ppm and total alkalinity of 50–90 ppm. The epilimnion extends to a depth of about 6 fath in midsummer with a mean temperature of about 65 F. The metalimnion is typically quite thick with the temperature profile often complex. Internal seiches are common.

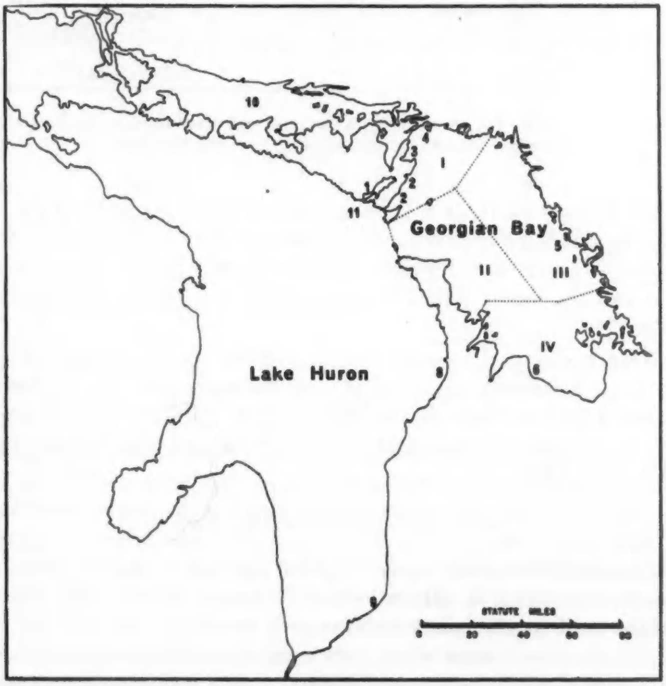

FIG. 1. Lake Huron and Georgian Bay. Roman numerals indicate the four districts of Georgian Bay; the study area, southern Georgian Bay, is District IV. Arabic numerals indicate whitefish tagging sites.

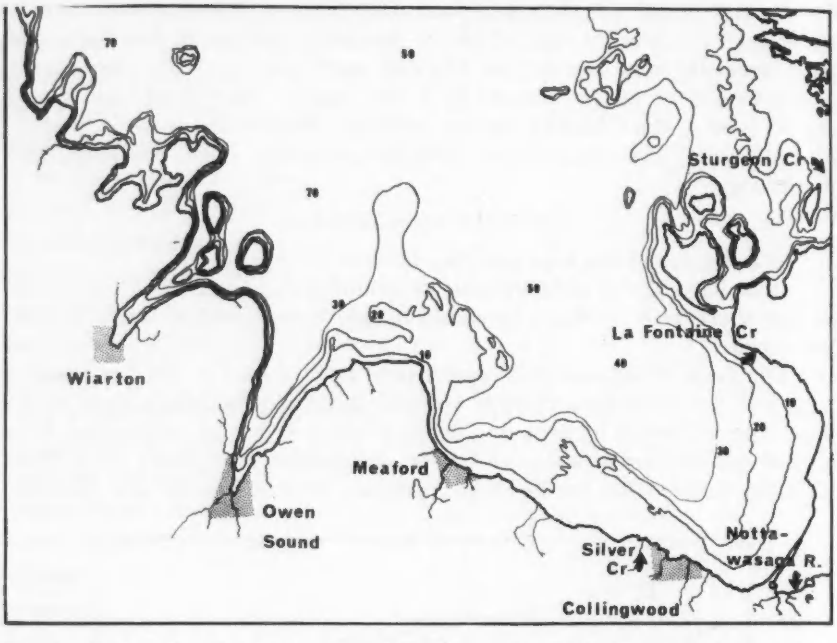

FIG. 2. Southern Georgian Bay showing depth contours, centers of human population (stippled), and streams utilized for spawning by sea lampreys (arrows).

Oxygen concentrations remain near saturation levels throughout the basi nat all times. The above generalizations are based on data collected by the Ontario Department of Lands and Forests (McCombie and Ryder, personal communications) and the Great Lakes Institute (Rodgers, 1960), and apply to the period since 1948.

No large population centers are located on the watershed of southern Georgian Bay. Industrial, agricultural, and domestic pollution is likely minor at all times, except perhaps at the mouth of the Nottawasaga River. Water samples collected near the mouth of this river indicated total dissolved solids of 296 ppm in July 1964.

DATA AND GENERAL METHODS

This report utilizes data on commercial catches, a tagging and sampling program, an experimental gillnet fishery in nearby South Bay, Manitoulin Island, and a mail survey concerning lamprey activity.

All area fishermen have since 1948 returned commercial catch statistics on the standard Great Lakes form (see Hile, 1962). Close contact with fishermen in the study area for a number of years convinced us that details are, with few exceptions, reasonably accurate.

A tagging and sampling program begun in 1956 has continued to the present (Table I). Fish for tagging were obtained from commercial pound nets. In 1956 the Department of Lands and Forests purchased total catches on a number of occasions and all live fish were sampled, tagged, and released. No fish were tagged in 1957, but a number were sampled. From 1958 to 1962 biologists accompanied the boats and tagged some or all sublegal fish (less than 2.0 lb total weight) taken in the nets. Sampling involved measuring length, removing scales, and sometimes weighing and sexing the fish.

Streamer type plastic tags were attached through the anterior base of the dorsal fin by means of monofilament nylon. The biologists tried to anchor the tag behind the interneural bone below the first dorsal fin ray. All fish tagged in 1961 had their left pectoral fins removed by clipping, those in 1962 had left pelvics removed.

TABLE I. Numbers of whitefish tagged and released in Georgian Bay District IV, 1956–64; also, estimated per cent of total catch of legal whitefish sampled.

		Per cent of total catch sampled		
Year	Number tagged	Spring gill nets	Pound nets	Fall gill nets
1956	1189	0	14	0
1957	0	<1	8	1
1958	331	1	60	2
1959	244	3	70	33
1960	445	7	89	25
1961	789	17	89	13
1962	412	8	75	15
1963	0	1	46	4
1964	0	3	78	10

Tagged fish recaptured in pound nets were generally released again if of sublegal size. When a biologist was aboard, many of the legal-sized fish taken in pound nets were examined and released again and the fishermen were compensated at market prices. Fish captured in gill nets were invariably killed.

Commercial fishermen were paid $1 for every tag returned with relevant data on locality and date of capture. A summary of the history of the tagged fish was sent to the fisherman who returned a tag. There is no evidence that fishermen purposely withheld tags or capture information, and they could not have benefitted in any way by doing so.

The commercial catch was sampled at all seasons of the year and from all fishing grounds. Generally a fisherman's total catch on a particular day was sampled. We judge the samples to have been reasonably representative of each season's catch.

Sampling methods were designed to interfere as little as possible with fishing operations. The market almost always preferred whitefish in the round (i.e. not eviscerated), so that data on sex, sexual maturity, stomach contents, and parasites could seldom be obtained.

The whitefish fishery utilized pound nets with 3-inch stretch mesh in the crib, and nylon gill nets of 4½-inch and occasionally 4¾-inch stretch mesh. Accurate estimates of the selectivity of these gears could not be obtained from project data. We assumed that the fish differed little morphometrically from whitefish in nearby South Bay, data from which were utilized by Regier and Robson (1966) to estimate gillnet selectivity.

A mail survey of fishermen was begun in 1954 to obtain data on incidence of lamprey scars in the commercial catch. Selected fishermen received data forms on which they were asked to indicate the number of fish of each species examined, number with healed scars, and number with fresh wounds. These data provide an index of lamprey activity and abundance.

As part of another study (Fry et al., 1960), some of the tagged whitefish were injected with a solution of lead versenate. Evidence is presented below that it had little if any effect on the health of the fish.

The methods used in this study to age whitefish closely resemble those described in some detail by Christie (1963).

COMMERCIAL FISHERY, REGULATIONS, AND PRACTICES

Information on the early fisheries of Georgian Bay is contained in annual reports of the Canadian Department of Marine and Fisheries and in the 1905–08 Georgian Bay Fisheries Commission report (Birnie et al., 1908).

Native American Indians long ago fished Georgian Bay waters using gill nets of cedar withes. A commercial gillnet fishery was begun about 1834 using cotton or linen mesh fished from canoes or small boats. Steam tugs were introduced between 1870 and 1875 and the steam gillnet lifter about 1890. Nylon gill nets first appeared in 1950 and the change was essentially completed in 1953. Pound nets first appeared about 1883. Use of seines and trap nets was early made illegal for commercially valuable species, but at least a few seines were used occasionally and illegally until the early 1930s. Seining for coarse fish was permitted but was done only intermittently. The "deep trap net" (Van Oosten et al., 1946) was apparently never used in Georgian Bay. Since 1963 several trap nets have been licensed.

Besides forbidding the use of certain gears considered to be too destructive toward young or spawning fish of valued species, the government long ago passed laws regulating minimum mesh size, minimum fish size, maximum quantities of gear per fisherman, and areas in which specific fishermen might operate. None of these laws was easy to enforce. Early annual reports of the Department of Marine and Fisheries testify that regulations, particularly those limiting amount of gear, were frequently violated.

Data on annual catches are available since 1868. But according to Birnie et al. (1908) the methods whereby early data were obtained were frequently imperfect; some catches were reported a number of times and others perhaps not at all. Thus early catch data are not very reliable. How rapidly the reliability improved over the decades is not known, but the consensus of fishermen and biologists is that data of the last two decades are quite reliable.

Following is a brief summary of current legal restrictions on southern Georgian Bay fishermen. A licence is issued for a particular gear, i.e. pound net, trap net, or gill net. Locations of pound nets and trap nets are specified. A gillnet licence is valid in only one or the other of the two districts, Simcoe and Grey-Bruce (Fig. 3). A gillnetter may not fish within ½ mile of a pound net, or in the Georgian Bay Game Fish Preserve (northeast corner of Fig. 3), or within 2 miles of the mouth of the Nottawasaga River. Only residents of the Indian reserves may fish within 2 miles of their shores — very few fish enter the commercial market from these reserves. Fishing in parts of the shoal area north of Meaford is legally restricted by the Department of National Defense but the restrictions have seldom been enforced in recent years.

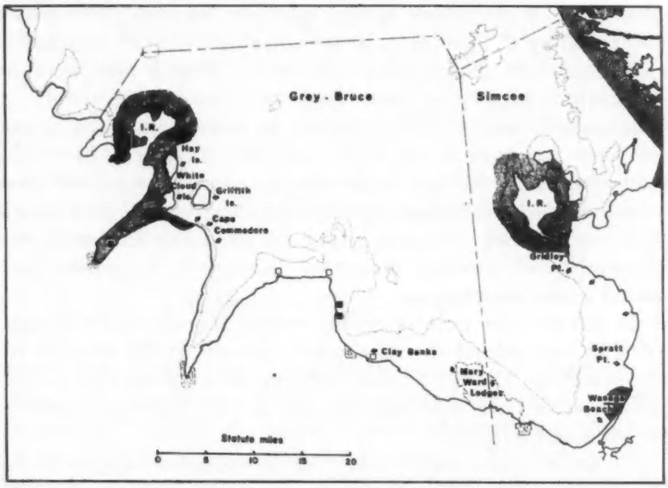

FIG. 3. Southern Georgian Bay showing the two administrative divisions of District IV, areas (stippled) where commercial gillnetting is not permitted, and reported whitefish spawning locations (arrows). Boxes indicate poundnet locations; those that are empty have not been fished since about 1940. I.R., Indian reserve.

A gillnetter may not fish more than the yardage licensed to him. Maximum length licensed is 48,000 yards of net. Minimum mesh size for whitefish and lake trout is 4½ inches, stretch measure. Lower legal size limit for whitefish is 2.0 lb in the round. There is no closed season. Annual licence fees are $20 for each 6000 yards of gill nets and $10 for pound nets and trap nets.

There has been for many decades a fear of overfishing and a newcomer has difficulty obtaining a licence. The fisherman must make monthly reports of his daily catch and specify location, type, and amount of gear fished, mesh size, species, and amounts caught, and prices obtained.

Lake trout and whitefish have been in approximately equal demand by the market and the fisherman throughout the past century in the study area. Nets frequently took both species and specific preference fluctuated seasonally. The usual annual fishing pattern is given below for the early 1940s, before the severe decline of the lake trout population. Details reported by Birnie et al. (1908) suggest that the overall pattern has held roughly constant since at least the beginning of the present century.

Gill nets were first set about mid April in 28–35 fath and these caught mostly lake trout. With calmer spring weather, fishermen followed the fish closer inshore and by the end of June were fishing in 16–20 fath and catching about equal quantities of whitefish and trout. Pound nets were set when weather permitted, usually in late May, and these took mainly whitefish during their inshore period. Fish returned to deeper water as summer progressed and were caught at about 20–23 fath, the two species in roughly equal numbers. Catches fell off in mid September and nets were removed until mid October. Lake trout were taken inshore on spawning grounds in early fall and whitefish in late fall. Fishermen then followed fish to deeper water and by mid December (if weather permitted fishing) both species were again taken in about equal abundance.

Only six pound nets were fished in recent decades and all were on the west shore. The east side of the Bay is too exposed to the weather to permit pound net operations. Leads of about 1000 yards were used with the cribs in 6–7 fath of water. Pound nets were usually set in May and removed when catches fell off about mid July.

Gill nets set in water deeper than 20 fath seldom caught economically satisfactory numbers of whitefish. Within the 20-fath contour, fishermen ranged over the shoals open to them. The shale substrate of the Mary Ward Ledges (Fig. 3) often tangled and tore nets so that fishermen seldom fished there. During the spawning season, from late October to early December, gillnetters followed whitefish inshore to a depth of 1–2 fath.

With the collapse of the lake trout fishery in the early 1950s, fishermen came to rely largely on whitefish supplemented by several species of ciscoes (*Leucichthys* sp.). Depths and areas fished were modified and the fishery has evolved toward a spring and fall system with little activity in summer.

The fishing industry has suffered from the low whitefish production of the late 1940s, the collapse of the lake trout fishery in the early 1950s, and the low whitefish catches from 1957 to 1962. Table II reflects this in the decline in the number of licensed fishermen operating in the two divisions of the study area. About one-third of the Simcoe fishermen and two-thirds of the Grey-Bruce fishermen operating in 1945 no longer fish. The Grey-Bruce grounds were traditionally better for lake trout, as shown in Table II, and thus suffered

TABLE II. Numbers of active gillnetters fishing the two divisions of southern Georgian Bay, and the whitefish catches as percentages by weight of the whitefish and lake trout landings in each division, 1945–64.

	Simcoe		Grey-Bruce	
Year	Number of outfits	Whitefish catch	Number of outfits	Whitefish catch
1945	43	59	47	20
1950	36	33	30	39
1956	39	95	31	67
1960	30	100	21	99
1962	30	100	16	100
1965	14	100	14	100

more from the lake trout decline. Many of the fishermen now operating do so only seasonally and supplement their incomes by other occupations during the remainder of the year.

COMMERCIAL CATCH STATISTICS

GEORGIAN BAY

Werner and Brubacher (1960) have summarized landings of various species from Georgian Bay since 1871. For most of the period, whitefish catches fluctuated around 1 million lb (Fig. 4). Two great bursts of production occurred but it is not clear to what extent these reflect either temporarily increased abundance, or increased effective effort, or both. The introduction of the steam-powered gillnet lifter in the 1890s certainly increased effective effort, and at least some of the increase in catches in the 1890s was likely due to this factor. Similarly, in the early 1950s fishermen changed to nylon gill nets and also changed fishing practices from those suitable for a mixed lake trout–whitefish fishery to an almost exclusively whitefish fishery.

Budd et al. (MS, 1963) state that in Lake Huron and northern Georgian Bay the 1943 year-class of whitefish was much larger than any others of recent years. It was, they state, recruited into the fishery over the years 1947–52. Growth data, given in a subsequent section, indicate that this year-class grew slowly, perhaps because of its abundance. Thus the low catches in the late 1940s were likely due to slow recruitment of this year-class into the fishery as well as the weakness of a series of year-classes before 1943. On the other hand the high catches in the early 1950s were obtained partly with an increase in effective effort due to a change from cotton and linen to nylon gill nets. McCombie and Fry (1960) found nylon nets to be almost three times as efficient as cotton with respect to weight of whitefish taken.

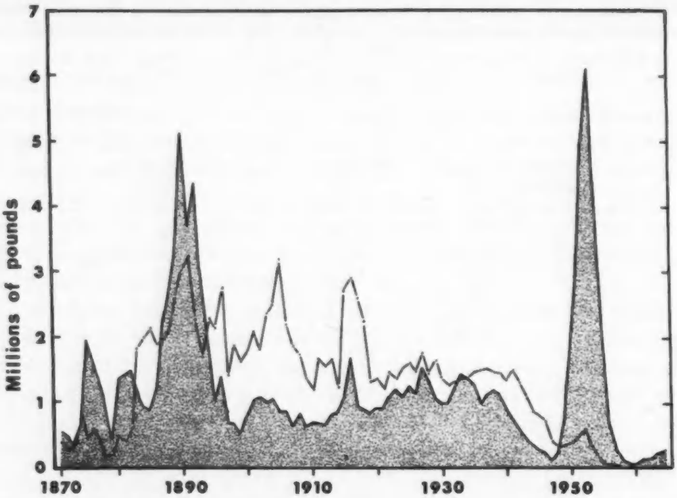

FIG. 4. Reported landings of lake whitefish (stippled) and lake trout from Georgian Bay waters, 1870–64.

SOUTHERN GEORGIAN BAY

Georgian Bay is divided into four districts (Fig. 1). Separate statistics for each district are available since 1948. District IV, the study area, has shown less violent fluctuations in annual whitefish landings than the remaining three districts (Fig. 5). Even so, the peak catch in the study area, in 1953, was 19 times the lowest catch, in 1948. Lake trout data (not shown) show a somewhat similar pattern in that production fell off more rapidly in the northern three districts than in the study area. Possible reasons for differences between districts are given in the discussion section.

The seasonal pattern of the fishery since 1948 may be inferred from the landings and effort listed in Tables III–VI. Fishermen have for many years eviscerated those fish that were dead for some time when the nets were retrieved. Since 1956, fishermen have reported total weight of such dressed fish separately from those marketed in the round. Since round weight was found to be 1.18 times the dressed weight, the reported landings of dressed fish were multiplied by 1.18 and then added to the reported landings of round fish to obtain corrected weights. Data since 1956 (not shown) showed that uncorrected landed weights were about 98% (range 95.6–99.0) of the corrected weights. Thus we expect that the data in Table VII on catch and catch per unit effort for the years before 1956 are underestimated on the average by about 2%.

The change from a fairly stable fishery during the ice-free period to one with peaks of production in May or June and in October or November with little between these periods is evident. This may indicate that whitefish stocks are now lower than before 1950 and it becomes commercially profitable to

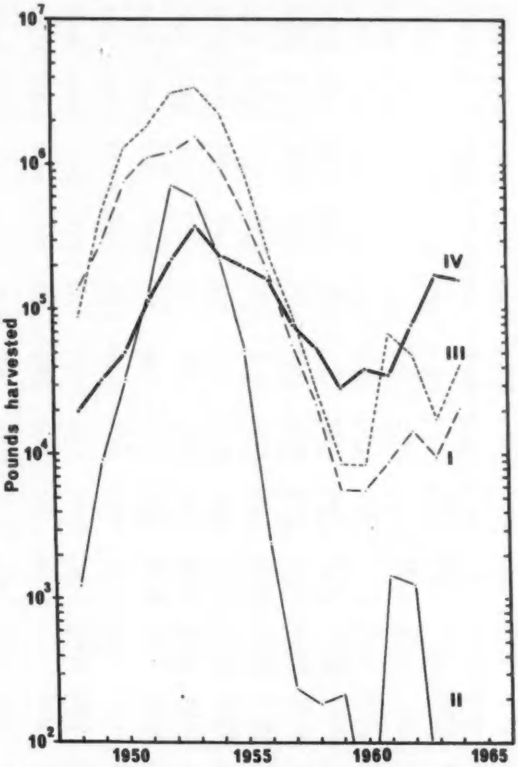

FIG. 5. Reported landings of whitefish from the four districts (Fig. 1) of Georgian Bay, 1948–64.

fish them only when they concentrate inshore and on shoals in spring and for spawning in late fall.

We have estimated the catch per unit of effective effort with 1000 yards of cotton net as a standard (Table VII). Efficiency factors are our "reasonable choice" based on what we know about relative efficiencies of nylon and cotton gill nets (about 2.9–1.0), the period of changeover (1950–53), and the gradual change in fishing practices from a mixed whitefish–lake trout to a whitefish-only fishery (1953–58) with an estimated increase in year-round efficiency of 50% in this period. The resulting estimates of catch per unit of effective effort (CUEE), we believe, reflect abundance levels more accurately than would catch per unit of reported effort.

Though we do not have effort data for years preceding 1948, we do know that licensed yardage remained approximately constant (between 1.47 and 1.65 million yards) from 1940 to 1958 (Werner and Brubacher, 1960). Market demand was consistently strong. Thus the low catch in 1948 (Fig. 4) likely re-

TABLE III. Reported whitefish landings in pounds, by gillnetters from southern Georgian Bay by months and fishing seasons, 1948–64.

	Year																
Month	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964
Jan.	–	–	–	–	–	370	1060	739	112	257	–	–	–	–	–	–	–
Feb.	401	–	–	–	–	–	–	37	235	–	–	–	–	–	–	–	–
Mar.	–	–	–	603	1948	8328	926	–	–	668	–	–	–	–	–	74	–
Apr.	–	440	–	4380	13061	32184	18412	12692	3654	5643	2358	–	1130	855	3643	1150	23970
May	2056	5401	7190	16779	30982	51587	37511	59457	21644	7954	8154	4326	14418	7660	15798	44193	36034
June	2609	7656	10111	19185	38577	52917	46475	50081	26479	8110	6262	2117	4127	3090	2111	20826	9296
July	3349	5632	7188	18236	21863	74272	36311	23872	19244	8880	5137	635	474	398	545	12169	15816
Aug.	2425	4143	7501	17732	38706	64181	42915	20626	10058	8239	7457	380	114	373	1275	8548	6569
Sept.	1924	2390	4562	9436	29793	32114	20384	8228	16766	5715	4629	142	137	1256	1561	4862	6303
Oct.	801	1080	2985	11375	16861	18865	14210	5070	14969	8822	6510	3663	5138	3438	15159	23014	23655
Nov.	1437	3691	6321	10921	18654	15235	9287	11909	13912	11935	9564	10993	9672	9972	23475	30689	20983
Dec.	4469	2116	4322	7144	14494	14389	3800	–	10198	5545	3330	2909	845	4771	8630	20368	11157
Spring[a]	10838	23272	31990	76915	145137	283844	183610	167504	81426	39751	29366	7458	20263	12376	23372	86960	94512
Fall	8631	9277	18190	38876	79802	80603	47780	25207	55845	32017	24033	17207	15792	19437	48825	84333	62098
Total:	19,469	32,549	50,180	115,791	224,894	364,442	231,390	192,711	137,271	71,768	53,399	25,165	36,055	31,813	72,197	171,293	156,610

[a] Taken to August 31 as this was approximately when the daily catches were lowest from 1955 to 1964.

TABLE IV. Reported gillnet effort, in thousands of yards, in southern Georgian Bay by months and seasons, 1948–64.

	Year																
Month	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964
Jan.	–	–	–	–	–	3.5	18.0	43.4	12.0	36.1	–	–	–	–	–	–	–
Feb.	45.5	–	–	–	–	–	–	0.9	7.5	–	–	–	–	–	–	–	–
Mar.	–	–	–	18.0	32.0	154.0	48.0	–	–	40.9	–	–	–	–	–	1.8	67.9
Apr.	–	61.3	–	161.6	341.7	499.2	533.3	316.0	66.5	231.6	81.8	–	29.0	21.9	103.9	31.0	273.5
May	312.8	444.6	458.8	526.3	674.3	897.4	1026.6	1061.4	723.9	288.1	360.1	185.5	258.6	224.1	396.2	599.1	537.6
June	284.3	724.3	508.9	485.1	790.1	923.1	1027.3	1253.9	717.8	280.0	273.2	123.7	111.7	82.5	124.1	420.7	187.2
July	497.8	531.6	485.7	641.4	607.8	1478.6	1215.6	1029.4	599.3	386.2	374.8	77.2	41.3	26.1	40.6	239.5	233.9
Aug.	470.5	471.1	382.7	585.8	738.1	1405.0	1375.5	870.3	473.3	411.8	346.4	74.6	14.4	37.1	86.6	376.1	186.3
Sept.	490.5	390.5	266.8	453.7	686.3	1022.5	565.3	400.6	710.6	366.5	208.0	53.7	17.2	61.6	64.0	243.4	168.5
Oct.	278.1	327.3	298.8	516.9	667.0	877.7	404.0	260.7	493.2	282.3	177.8	91.0	92.1	67.6	161.9	389.2	401.1
Nov.	261.7	273.0	267.7	401.1	389.1	541.1	179.8	309.2	294.2	136.3	135.4	130.8	121.4	170.3	256.0	398.4	346.7
Dec.	17.3	12.9	36.3	116.7	207.2	263.4	31.7	–	120.9	71.0	48.9	39.1	11.4	53.1	88.7	112.7	75.4
Spring[a]	1610.9	2232.9	1836.1	2418.2	3183.9	5360.8	5244.3	4575.3	2600.3	1674.7	1436.3	461.0	455.0	391.7	751.4	1668.2	1486.4
Fall	1047.6	1003.7	869.6	1488.4	1949.6	2704.7	1180.8	970.5	1618.9	856.1	570.1	314.6	242.1	352.6	570.6	1143.7	991.7
Total:	2658.5	3236.6	2705.7	3906.6	5133.5	8065.5	6425.1	5545.8	4219.2	2530.8	2006.4	775.6	697.1	744.3	1322.0	2811.9	2478.1

[a] Taken to August 31 as this was approximately when the daily catches were lowest from 1955 to 1964.

TABLE V. Reported whitefish landings, in pounds, by poundnetters from southern Georgian Bay by months, 1954–64.

	Year										
Month	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964
May	–	DNR[a]	347	297	121	–	260	–	1,164	1,350	119
June	–	DNR	11,722	3,945	1,940	2,144	2,105	1,958	4,402	6,018	2,210
July	1,567	DNR	10,051	2,971	1,775	1,396	918	1,211	1,304	2,395	447
Nov.	463	–	–	–	–	–	–	–	–	–	–
Total:	2,030	DNR	22,120	7,195	3,836	3,546	3,283	6,169	6,870	9,763	2,776

[a] Data not reliable.

TABLE VI. Reported poundnet effort in number of lifts, in southern Georgian Bay by months, 1954–64.

	Year										
Month	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964
May		DNR[a]	8	12	6	–	6	–	8	3	5
June		DNR	46	25	18	22	18	18	22	22	27
July	9	DNR	28	29	16	20	14	14	10	24	18
Nov.	9	–	–	–	–	–	–	–	–	–	–
Total:	18	DNR	82	66	40	42	38	32	40	49	50

[a] Data not reliable.

flects low abundance of legal-sized fish, probably lower than at any preceding date. CUEE was 7.3 lb per 1000 yards in 1948 (Table VII). Our estimates of CUEE for 1957–59 fall below this level and reflect, we believe, another low level of abundance. The data also suggest that the abundance in 1963 (Fig. 5), due largely to the 1958 year-class (see below), was not as high as that from 1950 to 1953, due to the combined 1943 and 1944 year-classes.

The data thus show that since 1945 there have been two oscillations of scarcity and relative abundance of legal whitefish following many years of relative stability.

TABLE VII. Gillnet catches of whitefish in southern Georgian Bay per unit of effective effort, 1948–64 (see text).

Year	Efficiency factor	Reported effort (10^6 yd)	Effective effort (10^6 yd)	Reported catch (10^3 lb)	Catch per unit effective effort (lb/10^3 yd)
1948	1.0	2.66	2.66	19.47	7.3
1949	1.0	3.24	3.24	32.55	10.0
1950	1.5	2.71	4.06	50.18	12.4
1951	2.0	3.91	7.82	115.79	14.8
1952	2.5	5.13	12.83	224.89	17.5
1953	3.0	8.07	24.21	364.44	15.0
1954	3.3	6.43	21.22	231.39	10.9
1955	3.6	5.55	19.98	192.71	9.6
1956	3.9	4.75	18.52	137.27	7.4
1957	4.2	2.80	11.76	71.77	6.1
1958	4.5	2.13	9.58	53.40	5.6
1959	4.5	0.78	3.51	25.16	7.2
1960	4.5	0.75	3.38	36.06	10.7
1961	4.5	0.74	3.33	31.83	9.6
1962	4.5	1.32	5.94	72.20	12.2
1963	4.5	2.81	12.64	171.29	13.6
1964	4.5	2.48	11.15	156.61	14.0

THE WHITEFISH POPULATION

In this section we present evidence on the discreteness of the population(s) in the study area and on migratory patterns within this area.

About 19,000 whitefish were tagged and released in Georgian Bay and Canadian waters of Lake Huron between 1949 and 1963 (Fig. 1, Tables VIII, IX). Recovery rates from the various years and tagging locations ranged from about 20 to 40%.

Budd (1957) analyzed data on tagging and found evidence of a number of populations or stocks in South Bay, Manitoulin Island, and Georgian Bay. These exhibited quite different migratory behaviour. The ranges of several overlapped geographically for part of the year.

Of special relevance to the present study is Budd's finding that, of about 15,000 whitefish tagged and released during 14 years in waters adjacent to southern Georgian Bay, only one was reported caught in the study area.

TABLE VIII. Data on whitefish tagging in Georgian Bay and Lake Huron.

Tagging location	Map location[a]	Years of tagging	Number tagged
South Bay	1	1949–63	13,711
Owen Channel	2	1951–63	2,029
Smith Bay	3		
Killarney	4		
Mink Islands	5	1951	52
Meaford	6	1956, 58–62	3,079
Wiarton	7	1956	329
Sauble Beach	8	1953, 56	200
Grand Bend	9	1958	177
North Channel	10	1961–2	650
Thomas Bay	11	1951	285

[a] See Fig. 1.

TABLE IX. Numbers of tagged whitefish released in the study area and tags returned by fishermen.

	Tags released		Tags recovered		
Location	Year	Number	Years	Number	Per cent
Wiarton	1956	329	1956–61	520	43.8
Meaford	1956	859	1956–61		
	1958	331	1958–63	147	44.4
	1959	224	1959–63	80	35.7
	1960	445	1960–64	159	35.7
	1961	789	1961–64	303	38.4
	1962	412	1962–64	165	40.0

Further, of about 3400 tagged fish released in the study area, only 12 were reported to have been caught outside the area. Thus the evidence is strong that the study area has been essentially closed to both in- and out-migration of older fish during the past decade. Whether this also holds for young-of-year or yearlings is not known.

Table IX refers only to those tags returned by fishermen from harvested whitefish. Many of the sublegal fish tagged during and after 1958 were recaptured shortly thereafter in the pound nets. These were almost invariably released again. Also many of the recaptures in pound nets the next spring after release were purchased by the Department and released again. As an example, of 412 fish tagged and released in 1962, 38 were recaptured within 1 month and again released. The next spring 93 were recaptured and 40 of these were again released. These 78 (38 + 40) fish are not a part of the datum 165 in Table IX.

In an attempt to detect a migratory pattern if one existed, all recapture data were separated by tagging location, year of tagging, age at recapture, and month of recovery; recapture locations were then plotted on a map of the study area.

Figures 6 and 7 show what we infer to have been the migratory patterns of the mature whitefish tagged in 1956 at Wiarton and at Meaford. Some whitefish had moved to the limits of the indicated range within 5 months of tagging. Tagged fish were caught thereafter throughout the range. As recaptured fish were not released at any location but the pound nets, we do not have direct evidence on whether there was an annual back-and-forth migration.

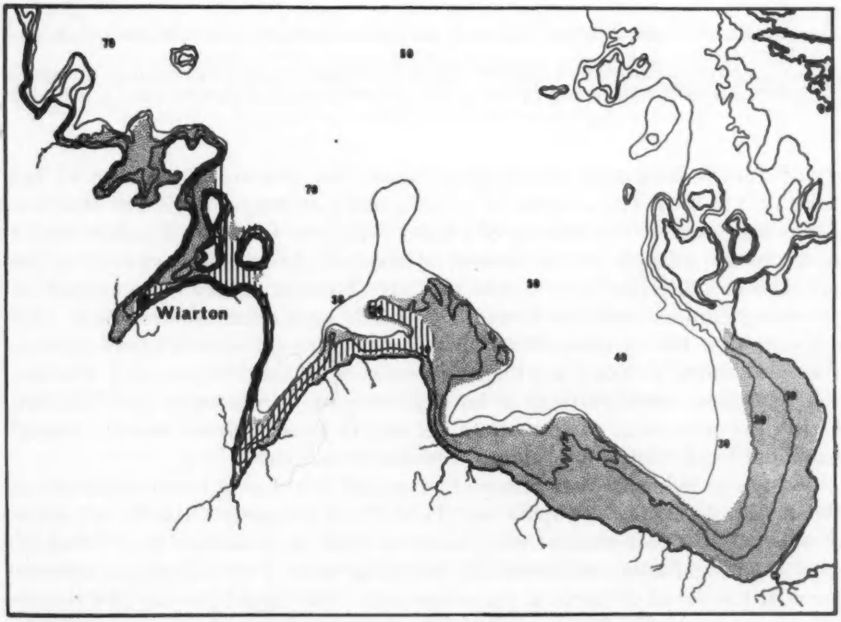

FIG. 6. Inferred distribution of whitefish tagged and released at Wiarton pound net in spring 1956, from 4 months after tagging throughout the remainder of their life span. Vertical bars, main concentrations; stippled areas, lower densities.

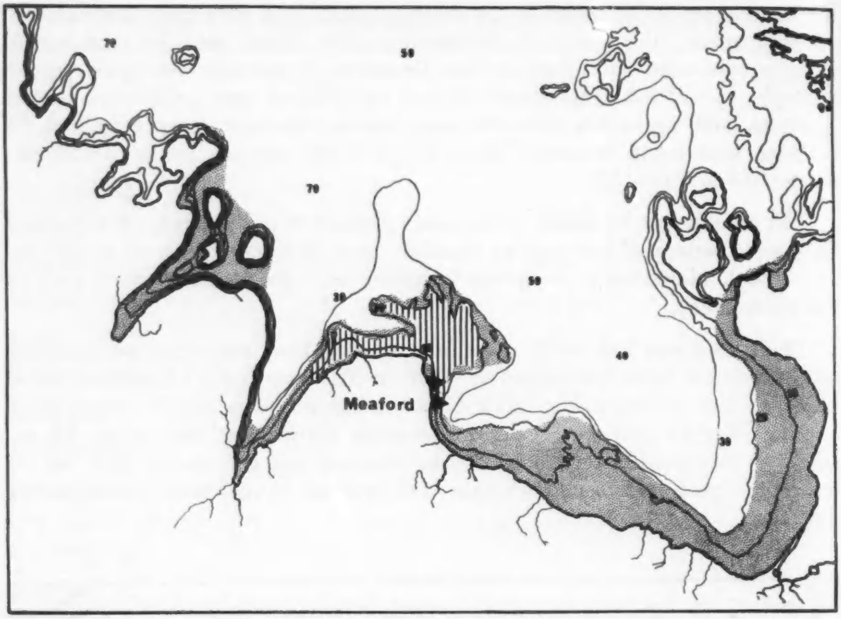

FIG. 7. Inferred distribution of whitefish tagged and released at Meaford pound nets in spring 1956, from 4 months after tagging throughout the remainder of their life span (see Fig. 6 for key to symbols).

Figure 8 illustrates the typical pattern for immature whitefish tagged from 1958 to 1963. The example is the 1954 year class tagged in 1958 at Meaford. In spring, most of the returns of tagged fish came from the Meaford pound nets and the gill nets within 10 miles of Meaford. In fall, most came from the gill nets set 30 miles away across the bay. The fall fishery concentrated on spawning grounds and few 4- and 5-year-olds were taken at that time. This suggests that few of these whitefish under 6 years old were sexually mature. (See a following section for a further discussion on sexual maturity.) The fact that in spring most whitefish older than 6 years were caught near Meaford and in fall most were caught across the bay is some evidence that an annual back and forth migration occurred between these areas.

There is evidence that behavior of tagged fish was not representative of the untagged part of the population (Table X). The data in Table X are typical of the 1954–59 year-classes; they were obtained as described in a following section on population estimates and mortality rates. Two differences between per cent harvested of the total year-class and of the tagged portion of the year-class are noteworthy. The tagged members entered the fishery earlier probably because the larger members of this year-class were tagged. Secondly, pound nets took a greater percentage of tagged fish than untagged, indicating either

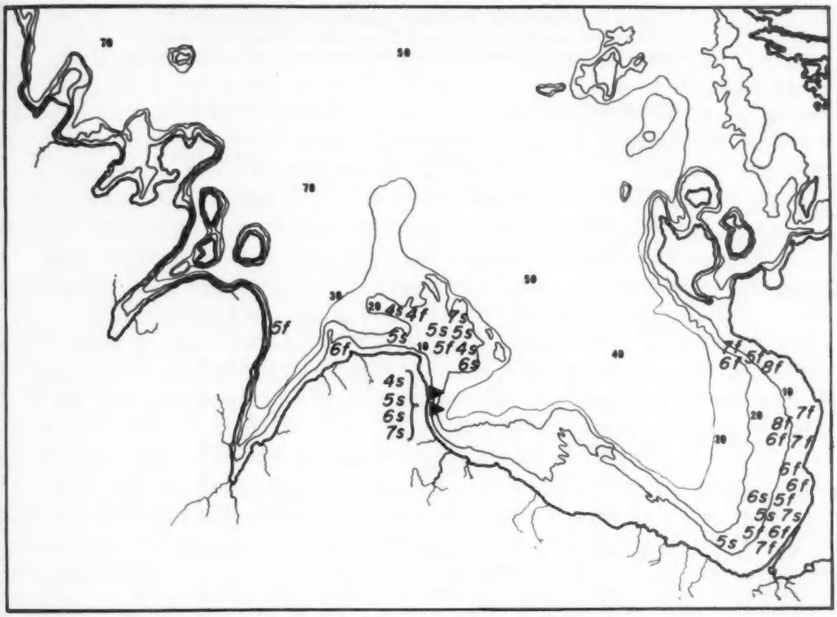

FIG. 8. Recapture locations of 1954 year-class tagged as immature fish in 1958 at Meaford. Number and letter combinations indicate locations, not numbers, of recaptures: numbers refer to age at recapture; letters to season, either spring (s) or fall (f). Bracketed symbols indicate recapture in pound nets; all other recaptures were made by gill nets.

that these fish tended to remain in the same general area year after year or tended to home to this area in June.

Bensley (1915), in discussing lake whitefish in Georgian Bay, stated: "In the southern part of Georgian Bay there is a tendency on the part of fishermen to recognize two types of common whitefish, one being called the coarse-scaled, shore or shoal whitefish, the other the deep-water whitefish. There are no whitefish inshore in the summer, and those that appear on the inshore shoals in November are recognized as shoal whitefish. The deep-water whitefish inhabits the deep water during the summer, but is thought to migrate northwards to the inshore shoals for spawning."

It may be that one of these stocks originated from hatchery plantings. Clark (1885) stated that whitefish from different lakes were easily recognizable before the hatchery program in 1875. Part of the evidence of the success of the hatchery program in early years was the fact that fishermen recognized some fish in their catches as being similar to those of another lake from which some stock had been introduced.

Fishermen no longer distinguish between two (postulated) stocks in the study area. The earlier presence of such a deep-water stock spawning in northern Georgian Bay would, however, provide an explanation for a number

TABLE X. Estimated per cent ages of extant members of 1954 year-class removed in each fishing season from total and from tagged populations (based on harvested fish only, as for Table IX).

Fishing season[a]		From total population	From tagged population
1958	SG	0	–
	SP	0.8	2.5
	FG	0	4.0
1959	SG	9.1	21.6
	SP	4.2	12.5
	FG	16.0	10.0
1960	SG	33.9	32.2
	SP	4.3	13.1
	FG	56.2	18.1
1961	SG	21.8	14.9
	SP	6.3	11.8
	FG	66.3	45.6
1962	SG	29.1	32.5
	SP	6.1	0

[a] S, spring; F, fall; G, gill net; P, pound net.

of phenomena. Thus, the very successful 1943 year-class found in northern Georgian Bay would move to the deeper waters of southern Georgian Bay to contribute to the fishery there. Similarly, a collapse of the deep-water stock in the late 1950s (see Fig. 5) would reduce catches throughout Georgian Bay. Its collapse would result in a poor deep-water summer fishery in the study area, as has been the case since 1956 (Table III). On the other hand, unless these stocks spawned in deep water, some would very likely have been tagged in the north (Fig. 1 and Table VIII). But only one of the northern tags was recovered in the study area. In short, this is an unsolved riddle.

We conclude that the population is not homogeneous but we do not know whether there are genetically discrete stocks present. If there are, then the data indicate that their geographic ranges must overlap for part of the year.

From an economic viewpoint it is important that at least part of the population has a migration pattern that takes it to all the fishing grounds in the study area. Thus, any attempts at management must be on an area-wide basis.

SEA LAMPREY PREDATION

The lamprey invaded Georgian Bay in the early 1940s. Lake trout production then began its steep decline (Fig. 4), and such a decline is generally conceded to have been a reliable barometer of lamprey build-up in the upper Great Lakes. A population of lake trout in the Grey-Bruce district survived for a number of years after those in adjacent waters of Georgian Bay and Lake Huron; this suggested that some grounds are protected by a partial barrier to lamprey, perhaps distance from a good spawning stream.

Surveys conducted by the Fisheries Research Board of Canada (J. J. Tibbles, personal communication) showed that four streams in the study area (Fig. 2) contained ammocoetes in 1964. The Nottawasaga River is the largest with a summer flow of about 400 ft^3/sec; ammocoetes were very abundant in it. Sturgeon Creek with 17 ft^3/sec had abundant larvae, Silver Creek with 6 ft^3/sec had moderate numbers of larvae, and La Fontaine Creek with 5 ft^3/sec had few. District III (Fig. 1) also had four lamprey streams but the nearest was over 30 miles from the northern border of District IV.

Lamprey attack whitefish, and at least some whitefish survive such attacks. Part of the routine sampling of commercial catches was the examination of fish for wounds and healed scars. Almost all the fish in the spring samples were older than 4 years and those of the fall samples older than 5 years. Table II shows that, except in 1960, per cent scarred and wounded fluctuated near a level of 3% from 1959 to 1964. Per cent with fresh wounds was higher in spring and summer than in fall.

The Nottawasaga River was treated with lampricide by the Fisheries Research Board in June 1961, and all other known lamprey streams in Georgian Bay were treated the preceding summer and fall. Lamprey predation should have been somewhat lower in 1961 than in 1960, and considerably lower in 1962, since the effect of the 1961 treatment of the large Nottawasaga would not be felt until 1962. Data on fresh wounds (Table XI) do not fully support this expectation. Thus per cent of the total annual catch bearing fresh wounds fell from 3.7 to 1.3 to 0.8 from 1960 to 1961 to 1962, but the actual number bearing wounds increased from 1961 to 1962. Whether number or per cent wounded is a better index of current lamprey activity likely depends on relative abundance of both species and thus it is not clear whether or not lampreys were actually less abundant in 1963 than in 1960.

Fishermen's replies to the mail survey (Table XII) agreed well with our data on injury only in the late fall. But the fishermen's spring samples most frequently came from gillnetters and ours more frequently from pound nets. Fish tangled in gill nets are more vulnerable to lamprey attack and this may help to explain the discrepancy. Also, in early spring and in midsummer, when fishing is poor (Table III), gill nets tend to remain unvisited for longer periods than when fishing is good.

Altogether the data indicate that since 1961 about 3% of adult landed whitefish had been attacked by lampreys and that over half of these had survived

TABLE XI. Numbers of whitefish examined for marks and per cent found injured by lampreys, 1956–64.

	Spring season[a]				Fall season				Total[c] injured		Total[c] wounded	
		Injured				Injured						
Year	Number	Total	Wound	Scar	Number	Total	Wound	Scar	Number	%	Number	%
1956	1188	1.9	ND[b]	ND	ND	ND	ND	ND	ND	ND	ND	ND
1957	204	4.4	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
1958	781	3.1	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
1959	965	6.3	3.5	2.8	1513	3.2	0.8	2.4	882	3.5	402	1.6
1960	1279	10.6	5.0	5.6	1009	6.6	2.1	4.5	3190	8.8	1345	3.7
1961	2273	4.4	2.3	2.1	804	2.1	0.6	1.5	953	3.0	953	1.3
1962	2800	4.0	1.7	2.3	2589	2.5	0.4	2.1	2156	3.0	593	0.8
1963	1961	3.5	1.5	2.0	1207	2.0	0.2	1.8	4730	2.8	1473	0.8
1964	1520	4.0	1.8	2.2	1792	1.7	0.5	1.2	4836	3.1	2012	1.3

[a] To August 31.
[b] No data available.
[c] Means; seasonal data were weighted by seasonal catch as in Table III.

TABLE XII. Numbers and per cent of whitefish in the study area reported injured by lamprey, fisherman mail survey, 1958–63.

Month	Number examined	Per cent injured
April	50	30
May	450	12
June	638	11
July	264	8
Aug.	132	19
Sept.	121	20
Oct.	474	6
Nov.	382	3

such attacks. Beyond this we do not know what effect lamprey have on the whitefish in the study area.

AGE AND SIZE AT SPAWNING

Data on age and size of males and females at spawning were obtained from fall samples. Sex was determined by external observation of the samples, since fishermen sold almost 90% of their catches in the round. Though males can generally be distinguished from females during the spawning season by their breeding tubercles, the emission of sex products was the only criterion by which sex was determined.

The whitefish catch was sampled at intervals throughout the fall fishing season but not according to a predetermined design. Fishermen actively sought spawning aggregations at this time.

During the years 1959–64, whitefish reproduction evidently depended largely on males age IV+ and older and longer than 17 inches, and females age V+ and older and longer than 18 inches (Table (XIII). Of the few age III+ fish taken, most were males. Of IV+ fish, large numbers of which were taken in 2 years, about 80% of the total for the 6 years were known to be males. Age V+ males also were obviously more abundant than females, comprising at least 60% of the catch. With fish age VI and older the evidence is ambiguous because of the large number of unknowns. Relatively few fish older than VIII+ were taken.

In the years 1962–64 evidently more females of age V+ and older were caught than in previous years. The references contain evidence (Miller, 1947) that faster-growing fish mature earlier than more slowly growing fish. The mean lengths of various age groups at time of spawning (Table XIV) do not indicate an increased growth rate and thus do not offer an explanation for the apparent earlier maturity in recent years.

The references (Christie, 1963) indicate that the distribution and movements of the sexes vary during the spawning season. In the absence of a sampling design, this was obviously not taken into account in obtaining samples. Thus, it may be that differences between years in Table XIII are due solely to differences in the timing of the sampling program.

The small number of fish under 16 inches caught on the spawning grounds is not merely a function of gillnet selectivity. For example, the efficiency at 15.5 inches was about 18% of that at 17.5 inches; but catches in the 15-inch stratum averaged only about 1% of those in the 17-inch stratum. We conclude that few of the smaller fish were on the grounds.

FECUNDITY

Data on fecundity (number of mature eggs per female) were obtained by sampling the catch from Woodland Beach spawning grounds during late October and November 1964. We limited the number sampled to five for each 1-inch stratum of fish length. Three samples were taken from each pair of ovaries

TABLE XIII. Per cent of whitefish, by ages and lengths, in samples from the fall fishery recognized as male and female, 1959–64.

	Age, *years*																				
	III+			IV+			V+			VI+			VII+			VIII+			≥ IX		
Year	No.	%♂	%♀	No.	%♂	%♀	No.	%♂	%♀	No.	%♂	%♀	No.	%♂	%♀	No.	%♂	%♀	No.	%♂	%♀
1959	5	0	25.0	63	52.4	3.2	490	60.8	4.1	128	57.8	8.6	203	64.6	12.8	311	64.0	18.3	303	59.1	23.1
1960	10	10.0	0	37	37.8	0	201	42.3	3.0	524	43.9	3.8	53	30.2	1.9	53	39.6	7.6	125	39.1	16.5
1961	14	78.6	0	454	79.8	2.9	107	74.8	2.8	93	44.1	9.7	78	44.9	21.8	13	46.1	23.1	43	53.5	27.9
1962	1	100.0	0	1412	81.0	6.1	1030	62.0	30.7	76	43.5	42.1	35	40.0	48.6	18	11.1	83.3	12	25.0	75.0
1963	4	25.0	0	43	74.4	4.7	1067	61.7	23.4	81	43.3	34.6	8	12.5	62.5	1	0	100.0	2	0	50.0
1964	3	33.3	0	129	62.0	2.3	560	61.1	10.9	1051	41.7	26.5	42	23.8	50.0	4	25.0	75.0	2	50.0	50.0

	Fork length, *inches*																				
	15.0–15.9			16.0–16.9			17.0–17.9			18.0–18.9			19.0–19.9			20.0–20.9			≥ 21.0		
Year	No.	%♂	%♀	No.	%♂	%♀	No.	%♂	%♀	No.	%♂	%♀	No.	%♂	%♀	No.	%♂	%♀	No.	%♂	%♀
1959	0	–	–	13	7.7	7.7	76	52.6	2.6	259	60.6	5.4	316	63.0	10.4	362	58.1	14.7	477	64.4	17.6
1960	1	0	0	8	0	0	24	25.0	0	100	46.0	3.0	227	40.1	3.5	319	44.2	2.5	324	39.5	9.6
1961	3	33.3	0	29	86.3	0	172	79.6	2.9	218	79.4	1.4	131	74.1	6.1	95	54.8	10.5	154	47.4	20.1
1962	6	83.4	0	163	75.4	8.0	793	81.3	7.8	824	73.4	14.8	489	59.2	31.1	211	56.4	34.6	103	40.8	52.4
1963	1	0	0	14	35.7	0	138	76.1	13.8	491	64.2	22.2	385	58.6	26.2	137	47.5	35.1	40	30.0	40.0
1964	0	–	–	11	54.5	0	99	59.6	7.1	377	61.5	11.4	593	49.1	19.9	405	46.9	24.9	215	30.2	30.7
Gill net selectivity[a]	0.18			0.61			0.98			0.90			0.56			0.26			0.12		

---

[a] For 4.5-inch nets; estimated at the mid point of each inch stratum.

TABLE XIV. Mean lengths of fall samples of whitefish by age and estimated per cent of total catch sampled, 1959–64.

Year	Per cent sampled	III+	IV+	V+	VI+	VII+	VIII+	IX
1959	32.5	16.8	18.3	19.0	20.0	20.7	21.1	21.4
1960	24.7	17.0	18.2	19.3	20.4	21.2	21.8	22.1
1961	13.4	16.7	18.2	19.7	20.6	21.7	21.5	23.1
1962	15.1	17.7	17.8	19.1	20.0	21.8	22.1	23.0
1963	2.8	16.8	18.0	18.9	20.2	20.8	22.7	24.4
1964	10.1	16.9	17.9	19.1	20.2	21.0	21.7	23.7

(each of which was intact), and total sample size comprised between 8 and 31% of the total weight of the ovaries, with a mean of 16%. Total eggs per female, $\hat{Y}_i$, were estimated using the ratio of weight of ovary to combined weight of sample.

To relate number of eggs to size of fish, Christie (1963) used the model $Y = aX$, where Y is number of eggs and X is fish weight in pounds. This model gave a reasonably good fit to our data, and age appeared not to contribute directly to the number. We computed $\hat{a} = \Sigma\hat{Y}_i/\Sigma X_i = 8212$ eggs/lb. To estimate the variance of $\hat{a}$ we followed Cochran (1953, sections 6.3 and 6.4) and simplified by setting $\hat{Y}_i = Y_i$, and $N - n = N$. We found $v(\hat{a})$ to be 211,398 and the 95% confidence interval of $\hat{a}$ to be 7252–9174 based on 22 fish weighing from 2.1 to 5.5 lb.

Our estimate of about 8200 eggs per pound is less than the figure of 9900 that Christie (1963) found for Lake Ontario whitefish and much less than the 16,100 found by Lawler (1961) for a sample from Lake Erie. The reason for these differences is not known but they may reflect an interaction of population density, and food availability. We doubt that these stocks would have maintained large genetic differences in the face of six or seven decades of hatchery stocking that deliberately mixed the stocks partly in hopes of producing "hybrid vigor."

LENGTH–WEIGHT RELATIONSHIP

We estimated separate length–weight relationships for fish caught in the spring and fall gillnet fisheries. Fish in the poundnet catch were sampled on board small boats where accurate weighing was impossible.

Five fish were selected at random from each 1-inch length stratum in each year. The data were pooled, transformed to logarithms, and a least squares regression calculated. The results were:

$$\text{spring,} \quad W = 0.0004713\,L^{3.0187};$$

$$\text{fall,} \quad W = 0.0002401\,L^{3.2093};$$

where W is weight in pounds and L is fork length in inches.

Kipling (1957) has shown that estimates of length–weight relationships based on gillnet samples may be biased due to the selection characteristics of the net. In particular the exponent of L tends to be underestimated and the coefficient overestimated. Such bias is reduced if the size range on which it is based is quite broad; in our case samples were obtained from 13 to 25 inches and this rules out the probability of an appreciable bias.

The length–weight relationship differed between spring and fall. Spring fish were heavier than fall fish, the difference increasing regularly from about 0.2 lb at 14 inches to 0.5 lb at 24 inches. The fall sample contained some spent fish and this may explain part of the difference.

SELECTIVITY OF THE FISHING GEAR

The only fishing gear used in the study area since 1956 were 4½-inch, and occasionally 4¾-inch (stretch), mesh nylon gill nets and pound nets with 3-inch tarred cotton mesh in the cribs.

Reliable estimates of the selectivity of these gears could not be obtained solely from the data available from the southern Georgian Bay population. Appropriate data are available for the nearby South Bay whitefish populations. McCombie and Fry (1960) estimated gillnet selectivity curves using South Bay data collected from 1954 to 1958; Regier and Robson (1966) have since based new estimates on more complete data collected after 1958.

Data from our study permit a check on the general accuracy of the selectivity curve for 4½-inch-mesh gill net by Regier and Robson (Fig. 9). In late spring of 1956, 1188 whitefish were caught in pound nets, tagged and released. These ranged from 12 to 23 inches in length and 4–13 years in age. Gill nets

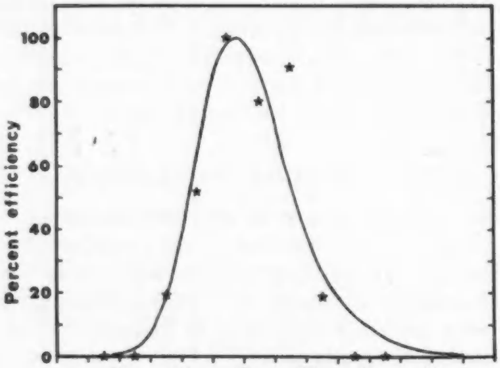

FIG. 9. Estimated efficiency of 4½-inch (stretch measure) gill nets to whitefish of different lengths (Regier and Robson, 1966). Stars are based on limited data from present study.

within 10 miles of the pound nets recaptured 101 of these before September 1, 1956. Data on lengths at recapture are not available, but growth data (see next section) indicate that average growth rate during the summer was about 0.2 inch per month. Thus if we take length at recapture equal to length at release we expect a maximum error of less than 0.5 inch and an average error of about 0.2 or 0.3 inch.

Selectivity of the gill nets was estimated by comparing the frequency distributions of lengths of fish released and of fish recaptured. In view of the small number of recaptures, data were stratified by 0.5-inch intervals. Table XV shows the data and estimated relative and per cent selectivities. The per cent selectivity data are plotted (as stars) on Fig. 9 and we consider the agreement reasonably good.

We know of no attempts to estimate the selectivity curve of pound nets towards lake whitefish. Van Oosten et al. (1946) give summaries by size of whitefish gilled in various mesh sizes of the cribs in deep-water trap nets. Judging from their data, tarred 3-inch mesh retains almost all whitefish over 2 lb and retains small numbers at 1 lb. According to the length–weight relationships of southern Georgian Bay whitefish, this implies an increase from a low efficiency at 12.5 inches to a high efficiency at 16 inches.

To test whether the efficiency of pound nets remains approximately constant beyond 16 inches, we compared the length frequencies of samples from gillnet catches and poundnet catches caught within 5 miles of each other during the spring and early summer in each of 1961 and 1962 (data not shown). If

TABLE XV. Estimated selectivities of 4½-inch mesh gill nets toward southern Georgian Bay whitefish. Data from 1956 tag releases and summer gillnet recaptures.

Length stratum (*inches*)	Number released	Number recaptured	Relative selectivity	Per cent selectivity
12.0–12.9	4	0	0	0
13.0–13.9	29	0	0	0
14.0–14.9	43	0	0	0
15.0–15.9	122	3	0.0246	19.1
16.0–16.9	256	17	0.0664	51.6
17.0–17.9	342	44	0.1287	100.0
18.0–18.9	244	25	0.1025	79.8
19.0–19.9	94	11	0.1171	91.0
20.0–20.9	42	1	0.0238	18.5
21.0–21.9	9	0	0	0
22.0–22.9	1	0	0	0

pound nets caught all sizes of whitefish over 16 inches with equal efficiency we should have obtained an estimate of the gillnet selection curve (by computing the ratios of gillnet catch to poundnet catch within various length strata) resembling that in Fig. 9. The agreement was good to about the 9-inch level, after which the data (based on relatively small numbers) fluctuated erratically above the expected curve and did not approach 0 until 25 inches. Van Oosten et al. (1946) found evidence that large whitefish do not tend to move inshore in early summer to the same degree that smaller whitefish do, and this might explain the discrepancy.

In summary, available data do not refute our assumption that the poundnet selection curve consists of an ogive from 0% at 12.5 inches to 100 at 16.0 inches and remaining constant at 100% beyond 16 inches.

GROWTH RATES

To estimate growth rates we corrected statistics from commercial catch samples for gear selectivity rather than by using scale proportions or data from tagged and recaptured fish. The estimates by our method apply to the mean sizes of the extant members of the population.

Gillnetters used 4½-inch mesh almost exclusively. These nets tend to select the larger members of a year-class until the year-class averages about 18 inches, and thereafter select the smaller members. Estimates of growth rate based on commercial samples corrected for selectivity are, as a result, biased downwards for 1 or more years (depending on the growth rate) after the year-class enters the fishery due to prior removal of faster-growing fish. Thereafter the removal of slower-growing fish tends to compensate for this.

The method of estimating a mean of the extant members of a year-class by correcting gillnet catch statistics for gear selection is as follows (Table XVI):

TABLE XVI. Calculations from length data on the 1955 year-class caught in the 1960 fall gillnetting season.

Length stratum (*inches*)	Observed frequency f_t	Efficiency factor e_t	Corrected frequency F_t	Stratum median	
				L_t	W_t
16.0–16.9	0	1.64	0	16.45	1.95
17.0–17.9	9	1.02	9.18	17.45	2.33
18.0–18.9	58	1.11	64.38	18.45	2.78
19.0–19.9	87	1.79	155.73	19.45	3.28
20.0–20.9	37	3.70	136.90	20.45	3.85
21.0–21.9	10	7.52	75.20	21.45	4.52
22.0–22.9	0	14.7	0	22.45	5.22
	$\Sigma f_t = 201$	$\Sigma F_t = 441.39$		$\hat{L} = 19.91$	$\hat{W} = 3.58$

Summarize the catch sample as a size–frequency distribution, e.g. by intervals of length. Let

i = subscript denoting stratum,

L_i = length at the midpoint of stratum i,

f_i = number of fish in sample of length L_i,

$\hat{e}_i$ = inverse of estimated relative efficiency of gill net to whitefish length L_i,

$\hat{F}_i$ = estimated relative frequency of gill net to fish of length L_i in extant population,

and $\hat{\bar{L}}$ = estimated mean length of extant members

Then

$$\hat{F}_i = \hat{e}_i f_i$$

and $\hat{\bar{L}} = \sum_i \hat{F}_i L_i / \sum_i \hat{F}_i$

Now $\bar{L}$ is the arithmetic mean length. To estimate the arithmetic mean weight, using a length–frequency distribution and length–weight relationship, estimate

$$W_i = aL_i^b$$

from the appropriate seasonal length–weight relationship and

$$\hat{\bar{W}} = \sum_i \hat{F}_i \hat{W}_i / \sum_i \hat{F}_i.$$

As we did not have a detailed estimate of the selection characteristics of pound nets, we did not correct estimates based on poundnet data. We assumed the nets were unselective for fish over 16 inches (see previous section). Below 16 inches the sample means are likely overestimates of the population means.

Growth data were summarized by year-classes (Fig. 10), ages being determined as in the following section. Certain features of the data were quite consistent. At smaller sizes (below 2.5 lb) the poundnet data tended to be higher than those from gill nets. At intermediate sizes (3–5 lb) the gillnet data were above those from pound nets. Thereafter they tended to be similar. These differences may be explained first by the fact that poundnet estimates under 2 lb (16 inches) are likely biased upwards; secondly, by the apparent tendency of larger whitefish to swim deeper and not move as far inshore in spring (Van Oosten et al., 1946; Kennedy, 1956); thirdly, by the likelihood that the larger fish of a year-class tended to mature earlier than smaller ones. We

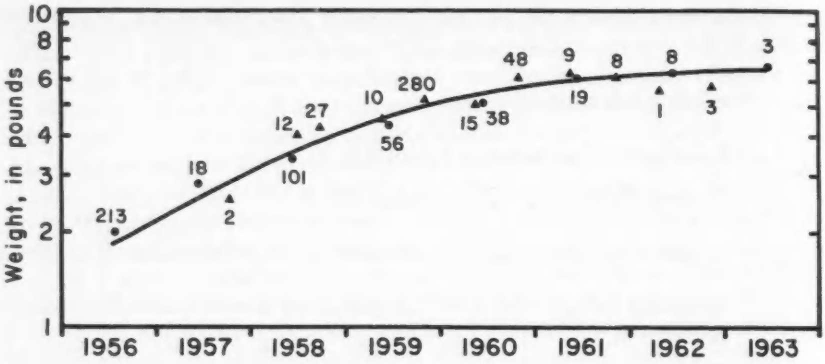

FIG. 10. Estimated weights attained by extant members of the 1951 year-class, 1956–63. Dots, simple means of poundnet samples; triangles, means of gillnet samples corrected for gear selectivity; numbers, sample sizes.

expect on these bases that with data above about 3 lb the gillnet estimates are high and the poundnet estimates low. Therefore, we simply fitted a line by eye to all the data of a year-class and believe that the line represents unbiased estimates of size attained by survivors of that year-class over the years.

Table XVII gives estimates of size attained by the year-classes 1943–59 on June 1 of the years 1956–64. The growth rates for the 1955–59 year-classes differed little. Earlier year-classes exhibited progressively decreasing growth rates. Thus extant members of the 1943 year-class only attained 3.5 lb at age XIII while those of the 1957 year-class averaged 4.0 lb at age VI. It may be objected that these data may simply reflect errors in aging. Reasons why we consider the aging to have been quite reliable are given in the next section.

A 4½-inch gill net tends to select larger members until the year-class averages about 18 inches or 2.8 lb. Thus the 1943 year-class apparently grew so slowly that survivors did not reach this size until approximately age XI, in 1954. As noted earlier, there is evidence that this year-class was recruited into the fishery during the years 1947–52 (Budd et al., MS, 1963). Thus, it was subject to selective harvests of its larger members for perhaps 7 years (with high effort in some years, see Table VII) before it reached the peak of the selection curve. Therefore, we expect that the apparent growth rate for the 1943 year-class as shown in Table XVII appreciably underestimates the true growth rate. We admit the possibility (but consider it improbable) that true growth rates of the 1943 and, say, 1955 year-classes did not differ, if the effects of gear selection alone might have yielded seriously biased estimates with the 1943 year-class. Instead, we infer that true growth rates increased markedly from the 1949–55 period to that after 1956, probably because of decreased population density. According to Table VII, the catch per unit of effective effort (CUEE) averaged about 12.9 lb/1000 yards in the 1949–55 period but only 8.2 in the 1956–62 period, a decrease of about 36%. This is evidence that population densities

TABLE XVII. Estimated weights, in pounds, attained by survivors of whitefish of the 1943–59 year-classes on June 1, 1956–64.

Year-class	Age															
	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII
1943	...	...	...	...	...	...	...	...	...	...	3.5	4.1	4.7	5.4	6.2	7.2
1944	...	...	...	...	...	...	...	...	...	3.4	4.1	4.7	5.5	6.4	7.4	...
1945	...	...	...	...	...	...	...	...	3.5	4.4	5.3	6.0	6.4	...	...	...
1946	...	...	...	...	...	...	...	3.5	4.7	5.6	5.9	6.2	6.5	6.7	6.8	6.9
1947	...	...	...	...	...	...	3.2	3.9	4.7	5.5	6.2	6.9	7.4	...	...	...
1948	...	...	...	...	...	2.9	3.7	4.4	5.1	5.8	6.5	6.9	7.1	7.2	...	...
1949	...	...	...	...	2.5	3.5	4.4	5.3	5.9	6.1	6.2	...	...	...	...	...
1950	...	...	...	2.2	3.1	4.1	4.9	5.5	6.1	6.3	...	...	...	...	...	...
1951	...	...	1.8	2.5	3.5	4.6	5.4	6.0	6.3	6.3	6.3	...	...	...	...	...
1952	...	...	2.1	3.2	4.1	5.0	5.5	6.0	6.5	6.9	...	...	...	...	...	...
1953	...	...	2.5	3.6	4.5	5.2	5.8	6.2	...	...	...	...	...	...	...	...
1954	...	1.9	2.8	3.9	4.8	5.7	6.2	6.5	...	...	...	...	...	...	...	...
1955	1.5	2.3	3.1	4.1	5.0	5.6	6.1	...	...	...	...	...	...	...	...	...
1956	1.4	2.2	3.3	4.3	5.0	5.5	...	...	...	...	...	...	...	...	...	...
1957	1.5	2.3	3.2	4.0	4.8	...	...	...	...	...	...	...	...	...	...	...
1958	1.5	2.3	3.4	3.7	...	...	...	...	...	...	...	...	...	...	...	...
1959	1.5	2.2	2.9	...	...	...	...	...	...	...	...	...	...	...	...	...
1960	...	2.1	...	...	...	...	...	...	...	...	...	...	...	...	...	...

were lower in the second period, and this may have permitted more rapid growth. With an increase in catch per unit effort from 1962 to 1964, growth rate apparently again declined somewhat.

In summary, data in Table XVII likely underestimate true growth rates until means reach about 4 lb, when gillnet selection for smaller fish may have cancelled out an earlier selection for larger fish. Pound nets were likely relatively unselective over 2 lb; in any case they took only a small proportion of the annual catch. Growth rate appeared to depend to some extent on population density.

Walford graphs (Ricker, 1958, section 9D), using mean lengths corresponding to the data in Table XVII, indicated that the von Bertalanffy model would yield reasonably good fits to these growth data, at least after the fish had attained a size of 16 inches. The mean asymptotic length was estimated to be about 24.7 inches, corresponding to 7.5 lb in spring and 7.0 lb in fall.

AGE COMPOSITION OF CATCH

We estimated the age composition of the catch in each of the three fishing seasons in each year: the spring gillnet fishery, the spring poundnet fishery, and the fall gillnet fishery. Commercial catches were sampled as described in the section on data (see Table I). All fish in each season's sample were aged and on this basis the age composition by weight of the total sample determined. Let

w_{ij} = weight of j th individual of age i in a particular season and

$$w_{i\cdot} = \sum_j w_{ij}.$$

Then $\hat{p}_i = w_{i\cdot}/\sum_i w_{i\cdot}$ = proportion by weight of age i in sample.

To estimate total weight of age i in commercial catch use

$\hat{W}_{i\cdot} = \hat{p}_i W_{\cdot\cdot}$, where

$W_{i\cdot} = \sum_i W_{ij}$,

W_{ij} = weight of jth individual of i year-class in the commercial catch, and

$W_{\cdot\cdot} = \sum_{ij} W_{ij}$ = total weight of catch.

To estimate age composition by number in the commercial catch, set

$$\hat{N}_i = n_i \hat{W}_{i\cdot}/w_{i\cdot},$$

where $\hat{N}_i$ = number of age i in commercial catch, and

n_i = number of age i in sample.

Table XVIII shows the age composition by number in the total annual commercial catch. Age composition of seasonal catch data are not shown, but were used in the mortality estimates described in the next section.

We did not attempt a detailed validation of aging. Both the biologists (D. Cucin and J. Smith) who examined scales had more than 5 years experience aging whitefish and had data on many tagged and recaptured fish to validate criteria. Questionable scales were aged independently by both, and they conferred on all differences before assigning ages. They considered many of the decisions on fish with apparent ages over 10 years as tentative.

There is internal evidence that some reliance can be placed on the aging, even of older fish. Reference to the 1943 year class has been made on a number of occasions; it was a large one in other areas of Lake Huron and Georgian Bay. The low catches in the period 1945–48 (Fig. 4) suggest that the year-classes 1939–42 were small. Table XVIII shows that only one fish of these year-classes was observed in the catch samples since 1956. But the 1943 year-class showed up in numbers in each year from age XIV to XIX. It should be emphasized that age data were not summarized as in Table XVIII until all aging was completed in 1963, and neither person had any preconceived notion that a strong 1943 year-class should be in evidence.

Further, the data indicate with considerable consistency from year to year that the 1954 year-class was moderately strong and the 1958 quite strong, while the 1947, 1953, and 1957 were all quite weak. If aging were subject to considerable error one would expect such differences to be largely erased. In short, we have some confidence the data in Table XVIII are sufficiently reliable for our purposes here.

The data show that in 1957 the fishery relied mostly on age VII–IX fish; by 1960 the main contribution came from ages V to VIII, and by 1963 from ages IV–VI. In 1963, 86% of the catch was age V; in other words, the fishery was dependent largely on one moderately large year class. There appears, therefore, to have been a "fishing up" between 1957 and 1964, from an earlier reliance on (perhaps) slower-growing, older fish to a later exploitation of rapidly-growing, younger fish.

TAG LOSSES

The streamer tag used was described in the section on general methods. Whitefish tagged in 1961 and 1962 were also fin-clipped. Some fin-clipped fish that had lost their tags were observed during commercial catch sampling (Table XIX).

To estimate rate of tag loss, we lumped data from individual years as shown in Table XIX, and assumed a loss rate proportional to number remaining affixed. We substituted these data in the appropriate maximum likelihood estimates (Robson and Regier, 1966) and solved iteratively. Details follow.

Let

j = subscript denoting year after original tagging and clipping;

TABLE XVIII. Estimated age compositions of annual catches, 1957–64.

Year	Age																	
	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	XIX
1957	0	0	13	682	897	5,447	8,432	4,694	1,905	1,531	98	36	170	0	0	0	0	0
1958	0	7	270	302	939	2,951	3,640	2,763	1,360	210	971	313	87	8	1	0	0	0
1959	0	28	670	3,089	795	952	1,349	750	398	68	83	51	39	6	43	0	0	0
1960	0	156	400	2,259	4,616	477	2,445	450	505	157	143	112	56	3	70	142	0	0
1961	5	290	6,609	1,370	12,97	965	133	129	134	139	77	59	7	0	0	0	7	0
1962	0	30	16,218	10,644	659	370	205	8	33	43	13	11	11	3	0	0	0	17
1963	10	183	2,538	52,702	5,291	282	26	14	22	7	7	0	4	4	4	0	0	53
1964	0	28	4,083	16,484	26,815	1,192	44	20	11	0	3	40	0	0	73	0	39	0

TABLE XIX. Data on number of fin-clipped fish seen by biologists and number that had lost their tags.

Tagging year	Recapture year	Number examined	Number lost
1961	1962	83	4
	1963	20	0
	1964	4	1
1962	1963	67	1
	1964	6	1

X_j = number of tags retained in sample of year j; and

$\hat{p}$ = estimated proportion of tags retained during 1 year's time.

We used the expression $\sum_{j=1}^{k} \frac{t_j \left(X_j - n_j \hat{p}^{t_j}\right)}{1 - \hat{p}^{t_j}} = 0.$

Trial and error iteration yielded the estimate

$$\hat{p} = 0.035.$$

In using data on tag returns to estimate population size and mortality rates in the next section, we needed to correct for tag losses.

To correct for tag loss, we assumed a constant exponential tag loss function, i.e.

$$\frac{X_o - X_t}{X_o} = e^{-\hat{\pi} t} = 1 - \hat{p}.$$

For our data $\hat{\pi} = 0.033$.

We then (Table XX) corrected the number of observed recaptures, R_i, in the ith time interval (e.g. 1963 fall gillnet season):

$$\widetilde{R}_i = R_i \, e^{\hat{\pi}(t_i - t_o)},$$

where $\widetilde{R}_i$ is the corrected number of recaptures and $t_i - t_o$ is the elapsed time between mark and recapture.

The Petersen estimate corrected for tag loss is then

$$\widetilde{N} = \frac{M \sum_i C_i}{\sum_i \overline{R}^i},$$

where M = number marked and

C_i = number of fish examined in ith time interval.

TABLE XX. Method of correcting number of tag recaptures for constant tag loss rate of 3.3%/year (mean tagging date was July 1, 1958).

Year of recapture	Date[a]	Proportion retained	Number observed	Corrected number
1958	0.60	0.999	1	1.00
	0.63	0.995	5	5.02
	0.79	0.990	7	7.07
1959	0.40	0.970	25	25.77
	0.50	0.965	2	2.07
	0.83	0.955	7	7.33
1960	0.39	0.940	18	19.15
	0.47	0.935	5	5.35
	0.84	0.925	5	5.40
1961	0.38	0.910	3	3.30
	0.49	0.905	2	2.21
	0.86	0.895	6	6.70
1962	0.32	0.880	2	2.27
	0.86	0.867	2	2.31
		Totals:	90	94.5

[a] Proportion of year elapsed.

POPULATION ESTIMATES AND MORTALITY RATES

We utilized the Petersen estimate corrected for tag loss to estimate numbers in the year-classes of 1943–59 at the time of tagging. From what we know about population distribution and movements, gear selectivity, distribution of fishing efforts, and tag loss rates, we believe that the assumptions on which the Petersen estimate is based were not seriously violated.

We obtained recapture data from the fishermen's tag returns, their daily catch statistics, and our catch sampling. We estimated the age composition of each fishing season's catch as shown in a previous section. Using the symbols and formula for the Petersen estimate as given in the preceding section, we set $C_i = n_i$ with the i's indexing the various gillnetting seasons following the tagging period (poundnet data were not included for reasons given below). Similarly, each R_i equals the number of tags returned by fishermen from gillnetted fish. In this way we estimated the number in the various year-classes at their respective mean tagging dates (the tagging period was always less than

6 weeks long). Concerning the accuracy of the R_i and C_i, we have no evidence that fishermen failed to return tags from harvested fish and first-hand observation indicated that the fishermen's catch statistics were quite reliable. In some seasons a relatively small sample of the commercial catch was sampled (Table I) and the respective C_i's were consequently less reliable than the others.

Two possible sources of bias should be examined further. As stated earlier, some of the tagged fish were injected with lead versenate as part of another study. Totals (Table XXI) were used to test the hypothesis of no difference between recovery rates for injected and noninjected fish using chi-square adjusted for continuity (Steel and Torrie, 1960, p. 371). As the calculated chi-square, 2.47, indicated nonsignificance at the 10% level, we inferred that the injections increased the mortality rates little if at all.

A second source of bias involves different vulnerabilities of tagged and untagged segments to the recapture gear. Table X showed that pound nets took a higher proportion of the tagged segment than of the whole population, and therefore relatively more than of the untagged segment. Gill nets took few tagged or untagged members of a year-class during the year of tagging since the fish were too small or did not frequent traditional gillnetting grounds. During the year after tagging, spring gill nets took relatively more tagged than untagged and fall gill nets relatively fewer. Thereafter, proportions were more nearly equal. This example is characteristic of all our data. A homing tendency that would bring tagged fish back to the gear where they were originally taken might well introduce a serious error in a Patersen estimate based on such recapture data. For this reason, population estimates (Table XXII) were based only on data from gill nets. However, all data on harvests (i.e. kills) were used to estimate natural mortality rates and per cent harvested during fishing seasons for a particular year-class, as in Table X.

TABLE XXI. Recovery rates of tagged whitefish injected with lead versenate and of noninjected fish.

	Not injected		Injected	
Year of tagging	Number released	Per cent recovered	Number released	Per cent recovered
1958	18	22.2	313	50.2
1959	148	34.5	96	31.2
1960	101	38.6	344	34.6
1961	534	34.5	254	43.7
Total:	801	34.7	1007	41.4

TABLE XXII. Petersen estimates of size of year-classes at indicated dates and ages.

	Tagging					
Year-class	Mean date	M_t	R_t corrected	C_t	$\hat{N}$	Age
1943+1944	July 18, 1956	20	3.25	639	3,932	XII,XIII
1945+1946	July 18, 1956	81	11.83	3,062	20,965	X,XI
1947	July 18, 1956	72	11.55	2,324	14,487	IX
1948	July 18, 1956	117	31.81	6,339	23,315	VIII
1949	July 18, 1956	322	95.22	11,842	40,045	VII
1950	July 18, 1956	282	94.80	10,494	31,216	VI
1951	July 18, 1956	213	66.84	5,831	18,582	V
1952	July 18, 1956	29	12.81	5,187	11,743	IV
1953	July 18, 1956	23	8.68	1,750	4,637	III
1954	July 1, 1958	169	84.32	8,141	16, 317	IV
1955	July 1, 1958	152	48.74	3,961	12, 353	III
1956	July 6, 1959	111	40.17	2,471	6, 800	III
1957	July 6, 1959	64	14.88	20,721	89,123	II
	June 25, 1960	390	114.68	20,698	70,389	III
	June 28, 1961	67	26.91	18,638	46,405	IV
1958	June 28, 1961	712	230.18	64,490	199,482	III
1959	July 1, 1962	175	21.58	7,282	59,052	III

We acknowledge that the argument in the preceding paragraph is to some extent circular, i.e. we rely on estimates based partly on Petersen estimates to validate the Petersen estimates. But there is further internal evidence in Table XXII that this method did not lead to serious error. The 1957 year-class was tagged in 1959, 1960, and 1961 and thus permitted population estimates in the 3 years. Nevertheless, the three sets of estimates of per cent harvested in each season, with these estimates based partly on three different population estimates, were remarkably similar in spite of the fact that in the year after tagging the three groups exhibited somewhat different distributions and movements. We make two inferences from this agreement: that fish of ages V and VI behaved similarly whether they were tagged at age II, III, or IV and that population estimates were approximately correct. We consider this a more reasonable explanation than the alternative, namely that the method, though perhaps seriously inaccurate, somehow generates similar estimates of the sort shown in Tables X and XXV.

For estimating natural mortality rates, we assumed the usual exponential natural mortality rate in the absence of fishing. We used the method described by Regier (1962) to sort out natural and fishing mortality rates. In particular we used an extension of Regier's Model II-B, i.e. we took harvests in each fishing season to have been removed instantaneously on the mean dates of landings. Admittedly this is not a completely realistic assumption but two considerations indicate that resulting errors were not large. There are three fishing "seasons" each year. Since 1957, most of a season's catch has been taken in less than 4 weeks. These facts indicate that a frequently used alternative assumption, that fishing mortality coefficient is constant throughout a season (or even a year), is less realistic than the assumption here chosen.

We required two censuses of a single year-class to use this method of estimation. We had Petersen estimates of population size of the 1957 year-classes in 3 successive years and used these data to estimate mortality rates.

As a year-class ages it eventually ceases to contribute to the fishery. Where there is no evidence that these older fish cease to be vulnerable to the fishing gear (e.g. because of changed distribution, or becoming too large for mesh sizes used)[5] it is reasonable to assume that the year-class is practically extinct at that time. We made the somewhat more conservative assumption that, during the last season in which a year-class is observed to contribute to a fishery, one-half the population escapes the fishery. We then had estimates of population sizes on at least two dates for each of the year-classes listed in Table XXII and estimated the average natural mortality rates applicable to the intervals between dates (Table XXIV). Where population size at the first estimate was quite large and a number of years intervened before the last estimate, even a five-fold difference in population size assumed to be present on the last date (e.g. 20 vs. 100) would not markedly affect the mortality rate estimate.

Also, we used the above method restricting the data only to tagged fish. The number of tagged fish released was then a known population size at one point in time. We doubled the last reported catch of tagged fish for the second "census" (tag recapture data were corrected for tag loss as shown in Table XX).

We first used the graphical method described by Regier (1962) but found it tedious and lacking in accuracy. An iterative solution was programmed for an electronic computer (Table XXIII). Iterations were continued until succeeding estimates of mortality coefficients did not differ by more than 0.0005. The computer calculated the estimated population ($\hat{N}$) just before each (instantaneous) fishing season and the estimated proportion of the extant population removed ($C/\hat{N}$).

In Table XXIV each mortality rate applies to only one year class and the period indicated except that the 1943–45, 1946–47, and 1952–53 year-classes were combined since small numbers were tagged.

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[5] As a check on whether larger fish were present, we fished some 5-inch mesh nets during the 1964 fall gillnet fishery. We found no evidence of the presence of fish too large to be taken by the 4½-inch mesh.

TABLE XXIII. Output of electronic computer programmed to estimate mortality rate of 1954 year-class from estimated population on July 1, 1958 (i.e. 0.50) and catches from 1958 to 1963.

Date	$\hat{N}$	C	$C/\hat{N}$
0.50	16,317	0	0
0.52	16,221	135	0.008
0.84	14,640	0	0
1.43	12,306	1,114	0.091
1.48	11,029	467	0.042
1.86	9,444	1,508	0.160
2.38	6,810	2,308	0.339
2.48	4,371	189	0.043
2.83	3,773	2,119	0.562
3.41	1,394	304	0.218
3.47	1,071	67	0.063
3.86	895	594	0.663
4.39	257	75	0.291
4.46	179	11	0.061
4.85	149	119	0.794
5.45	26	0	0
5.47	26	14[a]	0.544
5.48	12[a]	0	0

Number of iterations = 10

Natural mortality coefficient, 10th iteration = 0.29404

Natural mortality coefficient, 9th iteration = 0.29434

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[a] Further iterations would be required to make these two data equal, to correspond to our assumption. This would result in a correction at the fourth significant figure in the natural mortality coefficient, a degree of accuracy not warranted by the data.

It was possible to estimate natural mortality coefficients for both the total population and the tagged segment in seven instances. These estimates are not statistically independent since they ultimately utilize some of the same data, i.e. number recaptured, but to what extent they are correlated is unknown. Three of the seven estimates agree closely; three of the remaining four are based on relatively few tag releases. Giving all of these 14 estimates equal weights, we estimated that the natural mortality rate of the tagged segment

TABLE XXIV. Estimates of natural mortality coefficients and per cent expectation of death in the absence of fishing for the total population and for tagged segments for a series of year-classes over specified periods.

			Nat. mort. coeff.		Per cent expectation	
Year-class(es)	Mortality period	Tags released	Total	Tagged	Total	Tagged
1943–45	1956–59	56	–	0.699	–	50.2
1946–47	1956–60	117	–	0.632	–	46.8
1948	1956–61	117	–	0.463	–	37.0
1949	1956–60	322	–	0.505	–	39.7
1950	1956–61	282	–	0.479	–	38.1
1951	1956–61	213	–	0.483	–	38.3
1952–53	1956–60	52	–	0.353	–	29.7
1954	1958–62	169	0.294	0.293	25.4	25.3
1955	1958–63	152	0.377	0.372	31.4	31.1
1956	1959–64	111	0.310	0.424	26.7	34.5
1957	1959–60	64	0.259	–	22.8	–
	1959–61	64	0.335	–	28.4	–
	1959–64	64	0.393	0.553	32.5	42.5
	1960–61	390	0.407	–	33.3	–
	1960–64	390	0.451	0.461	36.3	36.9
	1961–64	67	0.546	0.345	42.0	29.1
1958	1961–64	712	0.409	0.514	33.5	40.0

of the population was 1.029 times that in the total population. Student's *t* (Steel and Torrie, 1960, p. 179) showed that this estimate did not differ significantly from unity. Thus the evidence suggests that tagged fish did not suffer markedly greater natural mortality rates than untagged fish.

The largest estimated natural mortality coefficients were obtained from the oldest fish, those of the 1943–47 year-classes, tagged in 1956. There appeared to be little trend with age or time in the data for the 1948–58 year-classes. In this latter group, the coefficients ranged from 0.26 to 0.55 with a mean (unweighted) of 0.41.

In terms of annual expectation of death in the absence of fishing (see Ricker, 1958, for discussion), the range was 23–42% with a mean of 33.6%.

Table IX shows per cent of tags attached in various years subsequently recovered by fishermen. The 1956 lot included a broad range of ages at tagging, subsequent lots were almost all sublegal fish of ages II–IV. The data show that fishermen captured from 35 to 45% of these fish subsequently to tagging.

As stated earlier, part of the computer program (Table XXIII) involved estimation of proportion of extant population removed in each fishing season (Table XXV).

Three separate estimates (though not statistically independent) were available for certain ages in the 1957 year-class. The 1957(59) estimates utilized a Petersen estimate based on the 1959 tagging releases; the 1957(60) estimates on 1960 releases; and so on. There was close agreement between estimates of per cent harvested from each age group for the same period: 0.2, 0.1; 0.1, 0.1; and so on. We have argued above that this agreement permits some confidence both in the assumptions made and the methods used for obtaining these estimates.

We make several points about the data in Table XXV. Pound nets take a relatively small proportion of the population in a particular season (less than 7%, usually about 4%) but begin to take whitefish ½ year before the gill nets. Gill nets take quite a high proportion of the extant year-class when it attains a size that renders it at least moderately vulnerable to the gear — ages V, VI, and VII during the early 1960s. The data indicate that 40% or more of the

TABLE XXV. Estimated per cent of the 1954–58 year-classes harvested in each fishing season.[a]

	Year-class (year of tagging)													
	1954(58)		1955(58)		1956(59)		1957(59)		1957(60)		1957(61)		1958(61)	
Age	G	P	G	P	G	P	G	P	G	P	G	P	G	P
III	0	0	0	0	0	0.1	0	0.2	0	0.1	–	–	0	0
III+	0	–	0	–	0.3	–	0.1	–	0.1	–	–	–	0.1	–
IV	0	0.8	1.4	4.2	2.7	2.2	4.8	3.0	4.4	2.8	–	–	3.3	1.7
IV+	0	–	2.8	–	3.5	–	10.4	–	9.7	–	9.1	–	8.6	–
V	9.1	4.2	22.0	5.1	12.8	4.0	14.0	2.4	13.4	2.2	13.1	2.2	34.0	4.5
V+	16.0	–	23.3	–	32.2	–	40.9	–	39.9	–	40.6	–	–	–
VI	33.9	4.3	24.3	4.8	8.1	2.2	41.5	5.1	41.1	5.0	44.9	5.9	–	–
VI+	56.2	–	53.2	–	45.5	–	–	–	–	–	–	–	–	–
VII	21.8	6.3	23.3	3.7	18.0	2.4	–	–	–	–	–	–	–	–
VII+	66.3	–	76.7	–	–	–	–	–	–	–	–	–	–	–
VIII	29.1	6.1	–	7.0	–	–	–	–	–	–	–	–	–	–

[a] G, gill nets; P, pound nets.

survivors of a year-class may be removed in a single fishing season, and that this may occur in several successive fishing seasons. In one year, from age VI to VII, the 1954 year-class suffered an estimated 80% total mortality, and 85% of the deceased could be accounted for in the fishery. Similarly, between age VI and VII of the 1955 year-class (another fishing year) 77% died, 79% of these being harvested. For age V+ to VI+ of the 1957 year-class the data are 78% and 79%. These are the three most extreme cases, and they indicate that the fishery was efficient when a year-class became fully vulnerable to the gear.

Few whitefish mortality rates have been reported in the references. Neth (MS, 1959) found a natural mortality rate of 22% in an unexploited population in a small lake in the Adirondack Mountains of New York. Kennedy (1953, 1954, 1963) reported total annual mortality rates of 57–81% in four lightly exploited populations in four lakes of northern Canada and 61% in Lake Winnipeg when it supported a considerable fishery. All Kennedy's estimates were derived from catch curves based on samples from commercial gill nets. Catch curves based on gillnet samples must always overestimate whitefish natural mortality rates unless the fish fail to grow after they become fully vulnerable or a carefully designed series of meshes is used to provide a gear with equal efficiency towards all ages (sizes). The more rapidly they grow or the shorter the range in mesh sizes, the greater the error in the estimate.

With these considerations in mind, we believe that Kennedy's estimates are all biased upwards, and perhaps seriously so. On the other hand, Kennedy's estimates are based on catches of older fish and there is evidence in Table XXIV (mentioned earlier) that older whitefish in southern Georgian Bay suffer higher natural mortality rates than fish of intermediate ages.

Roelofs (1958), using catch per unit effort data, estimated a total annual mortality rate of 94% for age III and IV whitefish in northern Lake Michigan in the early 1950s. This is much higher than comparable estimates for our age III and IV fish, and somewhat higher than estimates for age V and VI fish discussed above. Roelofs felt that predation by lamprey was a serious mortality factor.

In summary, we believe a natural mortality rate in the absence of fishing of 34% in the study area to be a realistic one.

STANDING CROPS AND YIELDS

We estimated standing crop at a particular date by multiplying number in a year-class by mean weight and summing up the contributions of the various year-classes. Since smaller fish were not vulnerable to the gear, we estimated only the standing crops of whitefish either older than age III (or IV, V, etc.) or larger than 2.0 lb.

The problem was straightforward for 1956 since all age groups over III were tagged. In 1957 the commercial catch was not sampled, so that no estimate was possible. Thereafter only the sublegal fish were marked. By 1961 the fishery relied almost entirely on those year-classes tagged as juveniles. Thus we utilized the population estimates at the beginning of various fishing seasons from the computer output (Table XXIII) to estimate number in a year-class in any year after tagging. We used these data to obtain estimates of standing crops for the 1961, 1962, and 1963 seasons.

We estimated standing crops at June 1, the approximate mid point of the spring gillnetting season, but according to our model this was at the beginning of the first instantaneous harvest period. In reality the estimates would apply fairly closely to standing crops just before the spring netting season began.

We do not consider the estimates (Table XXVI) fully reliable, but believe they are approximately correct. For 1956, 1961, and 1962 the data for fish older than 3 years were very similar but that for 1963 was considerably smaller. Of more interest to the commercial fishermen are the data on fish larger than 2.0 lb, the minimum legal size; at 2.3 lb (about 17.5 inches), most become sexually mature and move into the intensively fished spawning areas at a size near peak efficiency for the gill nets used.

TABLE XXVI. Estimates of standing crops, in thousands of pounds, at the beginning of spring gillnetting seasons. Area frequented by whitefish was 311,300 acres.

Year	Older than 3 years	Larger than 2.0 lb	Larger than 2.3 lb	Commercial catch[a]
1956	426	370	334	160
1961	448	133	80	35
1962	429	407	248	78
1963	333	318	307	172

[a] For the calendar year.

According to these data, annual catches varied from 19% of the spring standing crop of legal whitefish in 1962 to 54% in 1963 with a mean for the 4 years of 36%. Comparable data for sexually mature fish are: range, 32–56; mean 45. These data are similar to those on per cent of survivors harvested during a fishing season and discussed in the previous section. Here the data are in terms of weight and are averaged over a number of year-classes.

Whitefish are taken from shallow depths near shore in spring and fall to depths of about 25 fath in late summer. The surface area of water in the study area, from 0 to 25 fath deep, was estimated from a hydrographic chart to be 311,300 acres. (This does not include shoal areas in the extreme northeast part of District IV, i.e. beyond the line with a compass bearing of 315° from Methodist Point. No tags were ever returned from this area and we infer that the whitefish population(s) under study did not frequent these shoals.) We consider Reighard's (1910) range of 10–35 fath in Georgian Bay as being inaccurate, at least for recent years.

On a per acre basis, standing crops of legal whitefish varied from 0.4 to 1.2 lb during the years shown in Table XXVI and commercial catches from 0.1 to 0.6 lb. For the 17-year period 1948–64, average commercial catch was 0.39 lb/acre. (No sufficiently detailed survey of the bottom has been made by which to estimate what proportion of the 311,300 acres might be inhospitable towards whitefish or yield little whitefish food. It is known that parts of the bottom are of exposed rock or shale and other parts are of clay.)

Estimates of standing crops in the absence of fishing were generated by two mathematical models (Table XXVII). The first model was based on mean rates estimated above, calculations being as follows. We arbitrarily began with 1000 age III whitefish on June 1; we subjected the fish to 33.6% mortality each year (i.e. natural mortality coefficient of 0.41); we used mean size attained by the survivors of 1955–59 year-classes at various ages (Table XVII) as estimated growth rate; and we multiplied survivors by mean weight to obtain biomass of extant population.

TABLE XXVII. Two models of the relationship of the total biomass of a year-class to age.

	Mean rates			Alternative rates		
Age	Number	Weight	Biomass	Number	Weight	Biomass
III	1000	1.5	1500	1000	1.5	1500
IV	664	2.3	1530	750	2.4	1800
V	441	3.3	1450	562	3.6	2020
VI	293	4.2	1230	422	4.5	1900
VII	194	5.0	970	316	5.3	1670
VIII	129	5.6	720	237	5.7	1350

The first model shows that the expected peak biomass of southern Georgian Bay whitefish year-classes should occur in the spring at age IV. Greatest (short run) returns would be obtained by intensively fishing ages III, IV, and V. Thereafter individual annual growth rate falls well behind natural mortality rates.

In the sections on growth and mortality, we argued that growth rates were likely somewhat underestimated and natural mortality rates somewhat overestimated. The alternative model was based on rates that we suspect err somewhat in the opposite direction, i.e. annual natural mortality rate of 25% in the absence of fishing, and growth rates as shown. Under this model the population peak at age V should be fished in ages IV–VI for maximum (short run) yields.

Table XXV indicates that fishing rates in the early 1960s effectively harvested ages IV–VI with an apparent trend to utilization of younger ages.

Comparing this with the two models indicates that exploitation levels were near the maximum short-run yields. These data do not indicate short-run overfishing.

We have emphasized the term "short run." The model based on mean rates indicates that optimum exploitation schedules would concentrate fishing on age IV fish. At this age relatively few females were sexually mature, so that optimum short-run exploitation would remove by far the greatest portion of a year-class before it reproduced. Whether this would reduce the probability of satisfactory reproduction is unknown, but we suspect it would. If it did then total standing crops (all ages) would on the average be lower than if exploitation centered on age V fish. This would provide "room" in the ecosystem for competitors, perhaps to the ultimate disadvantage of the whitefish.

The relationship of yield to fishing effort is of interest in considering ways of regulating a fishery. In southern Georgian Bay, gill nets have taken from 90 to 95% of the annual catch during the past decade (Tables III and V). The per cent of standing crop removed by gill nets and the gillnet effort for various years (Table XXVIII) do not suggest a close relationship between total reported effort and per cent yield.

TABLE XXVIII. Relationship of per cent of standing crop harvested in various years to total gillnet effort in thousands of yards.

	Per cent harvested by gill nets			
Year	>3 yr	>2.0 lb	>2.3 lb	Gillnet effort
1956	32.1	37.0	41.0	4219
1961	7.1	24.1	40.0	744
1962	16.8	17.7	29.0	1322
1963	51.4	53.8	55.7	2812

We attempted to relate fishing effort corrected for gill net selectivity, i.e. (effort) $(\sum_i f_i / \sum \hat{F}_i)$, to per cent by number of various year-classes harvested at fixed age but did not find close relationships (data not shown). Such attempts rest on a considerable number of estimates (gillnet selectivity curve, length–frequency distribution of year-class, Petersen estimate, mortality rate, year-class composition of catch, number harvested) and even relatively small errors in each could obscure a strong relationship.

In recent years the fishery has been largely limited to 2 months in spring and 2 in fall when whitefish distribution and behavior renders them particularly vulnerable to the gear. Under such circumstances, per cent of standing crop removed likely depends to a considerable extent on weather conditions and year-to-year differences in fish behavior as well as on effective fishing effort.

CLIMATE AND YEAR-CLASS STRENGTH

Christie (1963) found evidence that the strength of a year-class of whitefish in eastern Lake Ontario was related to November and April air temperatures. He calculated a thermal index in which he used mean monthly deviations from long-term norms as the basic data. The thermal index was obtained by subtracting each November deviation algebraically from that of the April next following.

We obtained data on monthly deviations of air temperature in the Georgian Bay area from the Canada Department of Transport's Meteorological Service and calculated thermal indexes using Christie's procedure. As a measure of year-class strength we used Petersen estimates at age III from Table XXII. The 1951–59 year-classes were used. Where the earliest estimate was of age IV or V fish, we simply extrapolated to age III assuming a 33.6% annual mortality (in each case these year-classes contributed very little to the fishery before the first population estimate).

There was no relationship apparent between year-class strength and the thermal index here calculated (Table XXIX). We tried other combinations of fall and spring temperatures and found no significant correlation. Miller (1956) found wind a serious mortality factor with whitefish eggs. It may be that southern Georgian Bay spawning grounds are more subject to wind action than those of Lake Ontario and this factor may have masked a relationship in the study area between year-class strength and the thermal index. Wind data for Georgian Bay were not examined.

TABLE XXIX. Comparison of year-class strength with a thermal index defined by Christie (1963) and with number stocked by Collingwood Hatchery (see next section).

Year-class	Number at age III	Thermal index	Number stocked, in millions
1951	40,500	3	4.60
1952	17,350	9	7.50
1953	4,640	−4	13.00
1954	24,110	−5	17.76
1955	12,350	4	9.68
1956	6,800	−1	3.91
1957	70,390	2	1.35
1958	199,500	2	0
1959	59,050	−3	0

EFFECTS OF HATCHERY PLANTINGS

The first whitefish hatchery on the Great Lakes began operations in 1875 on Lake Erie (Clark, 1885). Whitefish were introduced from Lake Erie into various other lakes and the resulting adults were, according to early reports, recognizably different from indigenous stocks and recognizable as being of the Lake Erie type (this was used as evidence of the success of hatchery plantings by Clark (1885)). Whether some Lake Erie fish were ever stocked in Georgian Bay is not known. A fish hatchery was operated at Collingwood (Fig. 2) from 1912 to 1957 and produced both eyed eggs and fry of walleyes and whitefish.

Christie (1963) has recently reviewed the literature on the efficiency of whitefish stocking programs and has presented evidence that such a program in Lake Ontario contributed little if anything to the commercial fishery. It was on the basis of earlier negative evidence (Dymond, 1957) in various waters that the Collingwood Hatchery was closed.

The Collingwood Hatchery over the years collected spawn in both Georgian Bay and Lake Huron proper. Part of the eggs were transferred to other hatcheries in some years and part of the fry and eyed eggs produced were usually stocked in waters other than southern Georgian Bay. Table XXX shows only the numbers stocked in the study area and Georgian Bay as a whole since 1930. Specific locations stocked varied from year to year but generally included the reported spawning areas (Fig. 3) and shoal areas off the various islands and points.

Comparison of year-class strength at age III with number of year-class stocked for the 1951–59 year-classes (Table XXIX) shows no apparent relationship.

Considered in the light of Christie's (1963) findings, our data gave no evidence that the whitefish population of southern Georgian Bay either benefited or suffered as a result of the hatchery plantings.

GENERAL DISCUSSION

This report is based on a project that had modest objectives, i.e. to obtain information on movements of stocks, on relative year-class strength, and possibly on mortality rates. Various features of the population and the fishery, however, indicated that the data once obtained might yield considerably more information than was at first envisaged. Another objective was then set, namely, to obtain evidence on possible overexploitation of the stocks. Though we do not consider the evidence to be conclusive we believe our data point to a relatively intense fishery and possible long-term overexploitation. Our discussion here concerns this problem. We forego detailed comparison of our ecological findings with those reported from other lakes. Even at best, reports of whitefish ecology and population dynamics have been fragmentary. Our findings are in general compatible with those reported elsewhere, some differences having been discussed in preceding sections.

TABLE XXX. Numbers of whitefish eyed eggs and fry from the Collingwood Hatchery stocked in southern Georgian Bay (SGB) and Georgian Bay as a whole (GB), 1930–57 (none was stocked after 1957).

	Number in millions			Number in millions	
Year	SGB	GB	Year	SGB	GB
1930	12.4	57.4	1944	22.5	58.0
1931	65.5	65.5	1945	14.1	38.1
1932	25.2	45.2	1946	3.0	42.2
1933	57.6	57.6	1947	0	30.0
1934	37.8	75.1	1948	0	23.8
1935	44.5	82.0	1949	13.1	41.1
1936	45.7	72.8	1950	1.5	31.2
1937	37.0	46.2	1951	4.6	55.1
1938	34.0	81.7	1952	7.5	50.0
1939	24.5	61.6	1953	13.0	54.5
1940	41.6	74.6	1954	17.8	62.8
1941	29.6	34.1	1955	9.7	46.7
1942	29.9	82.9	1956	3.9	8.9
1943	32.5	68.8	1957	1.4	ND[a]

[a] No data available.

We emphasize three ways in which an intensive fishery for whitefish may be inefficient. Individual year-classes may be harvested at too early an age, i.e. when individual growth rate exceeds natural mortality rates (the criterion here is essentially economic and is based on the assumption that value per pound to the economy does not depend on the supply, season, year, or size of fish). Secondly, a fishery may remove most fish before they are sexually mature and thus reduce reproductive success and subsequent yields. Thirdly, overfishing may release resources in the ecosystem (food organisms, or space) to undesirable competitors which, when more firmly established, may utilize sufficient of these resources or alter the ecosystem to reduce whitefish growth rates, reproductive success, survival, etc. We discuss these three possibilities in turn.

In the section on population estimates and mortality rates we showed that the fishery in the past decade, though quite intensive, was probably not inefficient on a short-run basis. Most of a year-class's contribution came shortly after the natural mortality rate had exceeded individual growth rate. We have not attempted a more sophisticated analysis (e.g. one that would yield an estimate of a eumetric fishing curve) partly because of the complexity of the problem. We know that catch per unit effort varies markedly from season to season and from year to year, that the fishing mortality coefficient is a complex function of time within a year, that growth rates vary in different years probably partly in response to density, that price obtained by fishermen varies, etc. Aside from this complexity, the result would be similar to that obtained with our simple analysis — a result which we do not find comforting when we recall the fate of many Great Lakes whitefish populations fished at ages II, III, and IV.

Concerning sexual maturity, we noted that even though considerable numbers of a year-class were taken before they became sexually mature, large numbers of ripe fish were captured on the spawning grounds and many must have spawned. In short, spawning escapement was certainly better than negligible. It is well known that large year-classes of whitefish can originate from relatively small stocks. But it is not known whether the probability of adequate reproduction is influenced by stock size. Population estimates in Table XXIX show that year-class strength is highly variable and may be weak for a series of successive years, e.g. 1952–56. But these data do not clearly indicate overfishing. Whether the gill nets fished on the spawning grounds seriously interfere with fish movement onto the spawning grounds is not known.

Thirdly, we have no data on abundance of other species in the ecosystem. The most effective competitor might be the round whitefish, but it does not appear to be very abundant. Miller (1947) found that the common sucker, another possible competitor, did not capitalize on an advantage offered by a very intensive fishery on whitefish. In short, we do not know whether some species are being given a competitive advantage to the disadvantage of lake whitefish by the fishery.

The three "direct" criteria used above do not indicate that southern Georgian Bay whitefish are being overexploited. Kennedy (1956) used what might be termed "indirect" criteria to judge the well-being of a whitefish stock. He compared his findings with those reported by Thompson and Bell (1934) on Pacific halibut. There is consensus among biologists that Pacific halibut were overexploited in the 1920s and that catch restrictions based on biological evidence were responsible for the satisfactory recovery of the fishery. The evidence that halibut were overfished is summarized by Kennedy (1956) as follows:

1. Total annual catch decreased in spite of increased fishing effort.
2. The original catch per unit of effort was at least eight times as great as it was after exploitation.
3. Over 40% of the stock of commercial fish was caught each year.
4. The average size of fish caught was much smaller than in the original condition and large fish were noticeably absent from the catch.

For the southern Georgian Bay whitefish, no records of catch per unit of (standard) effort are available for the first years of the fishery (about 1834).

But annual reports and other writings (e.g. Smiley, 1882, and Clark, 1885) of the late 19th century repeatedly indicate a falling off in catch per effort and in size of fish, a failure of inshore runs, etc., on the Great Lakes. Thus though we have no quantitative data on points 2 and 4 above, historical reports appear to agree with them. The quantitative evidence that we have on points 1 and 3 show that, if anything, southern Georgian Bay whitefish suffer more serious exploitation than Pacific halibut did. We estimated that an average of 45% of the standing crop of sexually mature fish were taken annually in recent years.

Some of the early reports of failures of spawning runs to enter inshore areas or streams related this failure to pollution, especially sawdust and industrial wastes. Eggs were sampled in some polluted areas, e.g. in the Detroit River; many were found but very few were alive. We know of no recent studies of the fertility of whitefish eggs deposited in the Great Lakes. It may be that whitefish and their eggs are particularly sensitive to pollution. Only very small parts of southern Georgian Bay are obviously polluted, e.g. some harbours, creek estuaries. The spawning grounds near the mouth of the Nottawasaga River may have been harmed, but other spawning areas (Fig. 3) have likely been little affected by pollution. Thus, we consider it unlikely that pollution is now a serious threat in these waters.

The likely adverse effect on whitefish of the lamprey invasion confounds a straightforward comparison on points 1, 2, and 3. Partial control of lampreys was effected in 1960 and 1961. If lampreys contribute significantly to natural mortality rates, then a shift in the peak of the biomass curve to a higher age is expected following lamprey control. If this does occur, then present levels of fishing intensity might result in short-run overexploitation.

Whether or not overfishing has occurred, present levels of fishing intensity have led to the almost complete reliance by the fishery on one or two year-classes. Year-class strengths vary widely in many whitefish populations and certainly in the present population. This leads to a boom-and-bust fishing economy, particularly if fishermen rely only partly on the stock for their livelihood and maintain large quantities of gear in readiness as they do in the study area. Whether a boom-and-bust economy is more desirable than a more regular economy is a political problem. Observed growth and mortality rates would yield approximately the same long-term production under either type of economy, provided that neither adversely affects reproductive success and the position of the whitefish in the ecosystem.

The southern Georgian Bay whitefish are at present one of the few moderately strong populations in the lower four Great Lakes. We suspect that this is partly due to relatively weak lamprey predation and partly due to the fact that relatively large areas of whitefish habitat in southern Georgian Bay are either legally closed to commercial fishermen or are unsuitable for fishing. The presence of such sanctuaries, and the probability that spawning occurs in some of these, places an upper limit on the exploitation rates. The relative area of such sanctuaries in the study area is much greater than anything that is available to whitefish in Lakes Erie, Huron, Ontario and Michigan — lakes in which whitefish populations are either at greatly reduced levels of abundance or almost extinct.

In conclusion, we believe that the whitefish fishery in southern Georgian Bay is quite intensive and that a further increase in fishing effort might well result in overexploitation if this is not yet the case.

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W. A. Kennedy and J. J. Tibbles of the Fisheries Research Board of Canada, London, Ont., respectively, reviewed the manuscript and provided data on lampreys.

J. R. Greeley of the New York State Conservation Department and N. S. Baldwin of the Great Lakes Fishery Commission reviewed the manuscript.

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Comparative Summer Limnology of Inner Long Point Bay, Lake Erie, and its Major Tributary[1,2]

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ABSTRACT

Long Point Bay, on the north shore of Lake Erie, is 28.2 square miles (7278 hectares) in area, with a maximum depth of approximately 10 ft (3.05 m). Big Creek, the major tributary, drains a watershed of 317 square miles (81,818 hectares), and discharges 4700 million cubic feet (127,000 million liters) of water into the Bay annually. Summer water temperatures in the Creek and the Bay were positively correlated with air temperatures in 1962. The water in the Bay was subject to considerable seiche action. Levels of nutrients and suspended materials were characteristically higher in the Creek than in the Bay. Gross reductions in levels of turbidity, total dissolved solids, nitrates, and phosphates occurred in the lower section of Big Creek and the adjacent area of the Bay. For example, phosphate levels of bottom samples were inversely correlated with those of water samples in lower Big Creek and its estuary. The path of Big Creek discharge through the Bay to Lake Erie was defined by an analysis of total dissolved solids and soil phosphate data.

INTRODUCTION

LONG POINT BAY, situated on the north shore of Lake Erie at 40°37′N lat, is one of the most southerly of Canadian waters (Fig. 1). The Bay has been formed by the continuous deposition of silt at a northerly bend in the characteristically straight original shoreline of the lake (Laidler, 1944). At this point of curvature, water action has formed a spit known as Long Point, some 20 miles in length.

A shoal extending from Turkey Point on the mainland to Pottohawk Point on Long Point has created a distinct Inner Bay of 28.2 square miles (7278 hectares) where the present study was undertaken. Because of favourable ecological conditions provided for warmwater fishes, furbearers, and waterfowl, Inner Long Point Bay and its adjacent marshes have been known as a haven for wildlife since the time of earliest exploration (Coyne, 1903). The area is extensively used for sport and commercial fishing, hunting, trapping, and aquatic recreation and, in recent years, has been the site of extensive cottage and tourist development. A study of the flora and fauna by Snyder (1931) established the area as a transitional life zone within the boundary between the typical Alleghanian and Carolinean conditions.

Inner Long Point Bay receives the waters of Big Creek, a major watershed draining 281 square miles (72,526 hectares) of agricultural land with an annual

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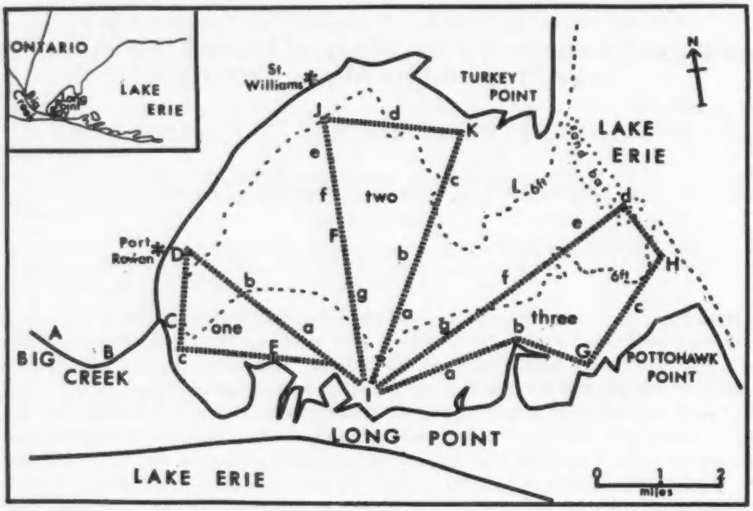

FIG. 1. Map of Long Point Bay and lower Big Creek showing locations of transects and sampling stations.

discharge of some 4700 million cubic ft (133,000 million liters) of water. Big Creek originally flowed directly into Lake Erie to the west of Long Point but, about 1834, it was diverted into Inner Long Point Bay. Local consideration is being given currently to the rediversion of Big Creek back into Lake Erie because of a presumed adverse effect on the Bay. The Big Creek watershed supports a major spawning run of rainbow trout which ascend each spring from Lake Erie although only its upstream waters are ecologically suitable for reproduction and the survival of progeny.

In spite of the importance of the aquatic resources of Inner Long Point Bay, virtually nothing is known of its limnology nor of the effect of Big Creek on its ecology and water quality. This paper reports on the first limnological study to be undertaken on the Bay. The study, carried out during the summer of 1962, provides a description of limnological conditions basic to an understanding of the productivity of the Bay and compares its limnology with that of the lower waters of Big Creek. The paper serves, also, to document existing limnological conditions with which future changes in the waters of Long Point Bay may be compared.

METHODS

A field laboratory was operated at Long Point Provincial Park from May to September 1962. Major study stations (A–L) were established in the lower part of Big Creek and at representative locations through Inner Long Point Bay (Fig. 1). Minor stations were located along three transects (I–III) joining up the major stations and giving a broad coverage of the Bay.

Air temperatures used in the study were recorded by the Long Point Climatological Station of the Meteorological Branch, Canada Department of Transport. Continuous recording thermometers for water temperatures were used at Stations B, C, D, and G. Subsurface and bottom water temperatures were recorded weekly at all major and minor Stations located on the transects.

Water levels were recorded continuously at the Port Rowan wharf (Station D) by means of a standardized Ott recorder. Staff gauges were located in the Bay at Stations C, D, G, and L. Flow measurements of Big Creek were taken by the Walsingham Gauge Station operated by the Water Resources Branch, Canada Department of Northern Affairs and National Resources, and supplemented by a staff gauge at Station B.

Field and laboratory studies were made weekly on water conditions at all major and minor Stations located on the three transects. Measurements included water temperature, colour, turbidity, transparency (Secchi disc), *p*H, conductivity, total dissolved solids, and total alkalinity (as $CaCO_3$). Water samples taken bi-monthly from Stations A–K were analyzed in the Toronto Laboratory of the Ontario Water Resources Commission for turbidity, total solids, B.O.D. (5-day), and nitrite, nitrate, ammonia nitrogen, and phosphate (total phosphorous as PO_4). The procedures used for all chemical tests were those outlined in the 11th Edition of Standard Methods for the Examination of Water and Wastewater.

Bottom samples were taken at 20 major and minor stations on June 19, and later analyzed for soil texture, *p*H, nitrate, phosphate (as P_2O_5), potash, and magnesium in the soil testing laboratory of the Department of Soil Science, University of Guelph.

OBSERVATIONS

PHYSIOGRAPHY

The drainage area of Inner Long Point Bay is 317 square miles (81,818 hectares) of which approximately 90% is covered by the Big Creek watershed. Big Creek, entering at the west end of the Bay, has a mean annual flow of 150 ft^3/sec (4245 liters/sec). The discharge of water from Big Creek into the Bay during 1962 is shown in Fig. 2. The mean rate of flow during the period of intensive study (May–September) was 81 ft^3/sec (2292 liters/sec) and varied between 65 and 112 ft^3/sec (1840 and 3170 liters/sec), reaching its annual low in late July, August, and early September.

In 1962, the water surface of Inner Long Point Bay was 28.2 square miles (7278 hectares), and the maximum depth was about 10.0 ft (3.05 m). Some 56% of the Bay was less than 6 ft (1.83 m) with an average of about 4 ft (1.22 m) in depth. The open water, i.e. that portion of the Bay studied, was bordered on the north, west, and south by marsh areas totalling over 10 square miles (2580 hectares), exclusive of extensive dyked marsh areas with controlled water levels to the west of the causeway linking Long Point with the mainland. The Inner Bay contained an estimated 4300 million cubic ft (122,000 million liters) of water.

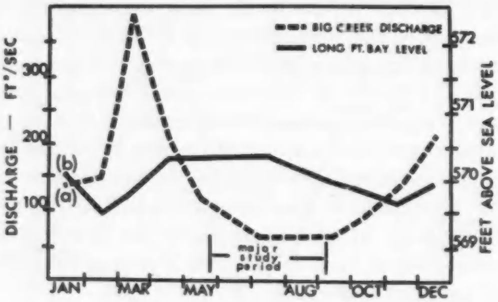

FIG. 2. Mean monthly data for (a) discharge from Big Creek and (b) Long Point Bay water level during 1962.

The bottom of the Bay was covered largely with black muck, often overlaid or mixed with clay or fine silt, except along the south shore (Long Point) which was characteristically hard sand often locally covered with black muck, occasionally mixed with sand. Virtually all areas with a soft or muck bottom supported aquatic vegetation and only local areas of wave-washed hard sand were free of plant growth. Approximately 90% of the bottom of the Bay was covered with aquatic plants which included, in order of abundance, *Chara*, *Valisnaria*, *Potamogeton*, *Najas*, *Nitella*, and *Anacharis*.

WATER LEVEL AND SEICHES

Because of the direct connection between Inner Long Point Bay and Lake Erie, the water level of the Bay is closely related to that of the open lake. Monthly mean water levels for the Bay in 1962 (Fig. 2) showed seasonal lows in February and November, and a high increasing from April to early July. The seasonal variation in mean water level was 0.8 ft (0.24 m) which was below the average range of 1.5 ft (0.46 m) between low and high water in any one year reported by Pincus (1962) for Lake Erie based on an analysis of records beginning in 1860. The present study of Inner Long Point Bay was done at a time when water levels were approaching a low in the long-range fluctuations characteristic of all the Great Lakes.

The mean daily discharge from Big Creek into Inner Long Point Bay between May 30 and September 6 was approximately 7 million cubic ft (198 million liters) or 0.1% of the total volume of the Bay water. Fluctuations in volume discharge from Big Creek did not affect appreciably the water level of the Bay which, rather, conformed closely to that of Lake Erie.

Seiche action was generally apparent in Inner Long Point Bay because of obvious short-period fluctuations in water level around the shoreline. Variations in a typical seiche recorded at the Port Rowan wharf (Station D) are given in Fig. 3. The maximum vertical displacement during this seiche was 1.53 ft (0.47 m). The mean period between peaks was 13.3 hr which corresponds closely to that of 13.16 hr reported by Reid (1961) for Lake Erie.

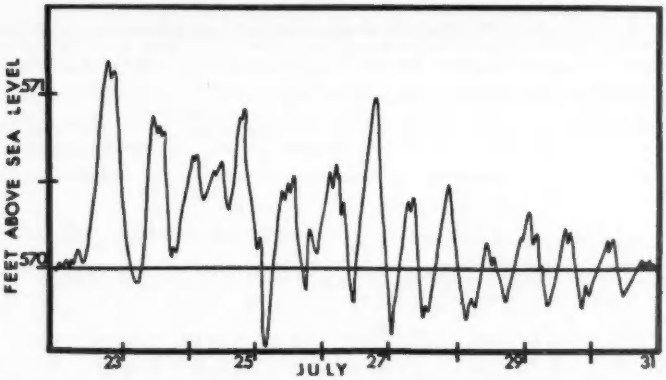

FIG. 3. A typical seiche record for station D, Inner Long Point Bay, July 23–31, 1962.

TEMPERATURE

Water temperatures recorded for lower Big Creek (Station A) between May 24 and September 6 ranged between 17.7 and 25.7 C and averaged 21.7 C for the period (Table I). Water temperatures in Inner Long Point Bay for the same period showed no evidence of any significant thermal stratification in the Bay water. As differences between subsurface (at 1 ft depth) and bottom temperatures were not observed to exceed 2.0 C at any time during the study period, water temperatures at the various Bay Stations may be considered homothermous for the purpose of comparison.

A comparison of water temperatures at the study Stations at weekly intervals indicated no appreciable horizontal difference in temperature levels within the Inner Bay. The mean water temperature of the Bay between May 24 and September 6 was 22.3 C, ranging from a low of 18.9 C on September 6 to a high of 26.5 C on July 8. The highest water temperature recorded at a Bay Station was 26.9 C at Station D on July 1.

Air temperatures for the corresponding period (Table I) showed a mean of 19.3 C, rising from a low on September 6 to a peak on July 8. The lowest daily minimum temperature was recorded on September 6, the highest maximum on July 8.

The relationship between air temperature and the water temperatures of both lower Big Creek and Inner Long Point Bay (Fig. 4) were tested by means of a regression model as described by Snedecor (1959, p. 160). A very significant correlation ($r = 0.89$) existed between the daily mean air temperature and the water temperature of the Bay. The degree of correlation was increased slightly ($r = 0.91$) by using the average of the means of air temperatures recorded on the day of the water temperature measurement and the previous day. This correlation may be compared with an r value of 0.97 obtained by Roelofs and Bumpus (1953) for Pamlico Sound. A similar analysis of the relationship

TABLE I. Mean air and water temperatures for Big Creek and Inner Long Point Bay, May 24 to September 6, 1962. Mean temperatures are those of the date specified; minimum and maximum temperatures are for the 5-day period ending on the specified date.

	Air temperature C			Big Creek temperature (Station A) C			Bay temperature (Station D, G, L) C		
		5-day			5-day			5-day	
Date	24-hr mean	Min.	Max.	24-hr mean	Min.	Max.	24-hr mean	Min.	Max.
May 24	15.3	–	–	22.5	–	–	19.6	–	–
May 29	15.6	12.8	15.6	22.1	21.1	22.1	18.9	17.1	19.7
June 3	14.2	11.9	20.0	22.4	22.4	24.6	18.7	17.8	20.9
June 8	18.0	15.0	18.0	22.8	21.1	22.8	23.1	17.1	23.1
June 13	14.4	13.9	20.6	20.2	20.2	25.7	19.1	19.1	25.1
June 18	21.1	16.1	21.7	23.3	19.1	23.3	24.7	18.9	24.7
June 23	21.1	15.8	21.1	20.4	18.5	22.1	23.5	21.5	23.5
June 28	21.1	18.9	21.1	21.1	21.1	22.4	23.8	23.8	24.9
July 3	20.3	20.0	22.8	21.2	21.2	22.4	23.2	23.2	25.5
July 8	25.0	20.8	25.0	23.1	21.0	23.1	26.5	22.9	26.5
July 13	20.0	19.2	21.7	22.3	21.2	22.5	23.4	22.1	24.3
July 18	21.7	19.2	21.7	22.3	20.8	22.3	22.0	22.0	23.5
July 23	19.4	19.4	21.1	21.9	21.9	22.4	21.9	21.9	22.5
July 28	20.8	16.4	21.1	20.4	20.3	21.6	19.5	18.6	22.0
Aug. 2	19.2	18.6	21.9	21.2	20.5	21.4	21.2	20.3	21.2
Aug. 7	21.7	20.8	23.3	–	–	–	24.8	22.3	25.2
Aug. 12	22.8	17.5	22.8	21.9	20.8	21.3	23.3	21.4	25.0
Aug. 17	18.0	18.0	21.3	21.8	21.2	21.2	22.3	22.3	23.6
Aug. 22	20.6	18.0	22.5	23.0	20.5	22.3	23.2	21.6	23.2
Aug. 27	19.4	19.4	24.4	22.9	21.2	22.9	24.6	23.0	24.9
Sept. 1	23.9	18.0	23.9	22.1	22.1	22.3	25.1	23.9	25.7
Sept. 6	10.5	2.0	19.5	17.7	17.7	21.5	18.9	18.9	24.3
Average:	19.3	15.8	21.5	21.7	20.7	22.5	22.3	21.0	23.8

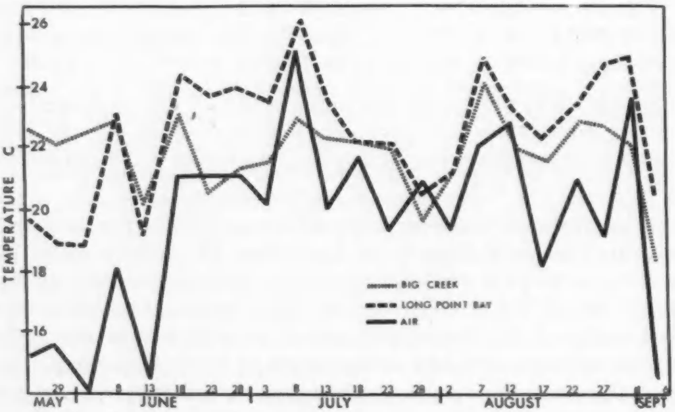

FIG. 4. Relationship between air and water temperatures of Inner Long Point Bay and lower Big Creek during the period of May 24–September 6, 1962.

between air and Big Creek water temperatures yielded much lower correlation coefficients of 0.66 and 0.72, respectively.

It is apparent from these coefficients of correlation, and visually evident in Fig. 4, that both the Creek and Bay water responded similarly to ambient air temperatures. However, variations in the water temperature of the Creek were less extreme.

HYDROGEN ION CONCENTRATION

The waters of both Big Creek and Inner Long Point Bay were alkaline, varying between 8.1 and 9.0 during the summer months (Table II). The highest values for both waters were recorded in late August and early September, the value of 9.0 reached in the Bay on August 22 approaching the upper limit of the *p*H range for natural waters (Juday et al., 1935).

TOTAL ALKALINITY

Total alkalinity levels for lower Big Creek were considerably higher than for the waters of Inner Long Point Bay. The seasonal average for the Creek was 174.8 ppm; for the Bay 66.8 ppm (Table II). No seasonal trend was apparent in either the Creek or Bay, nor was there any obvious differences among the Bay Stations. Total alkalinity levels fluctuated between 165 ppm (July 11) and 182 ppm (August 22) in the Creek, and between 59 ppm (July 11) and 86 ppm (June 27) among the Bay Stations.

TURBIDITY

Turbidity readings for lower Big Creek (average of Stations A and B) between May 24 and September 6 ranged from a high of 26.0 ppm on June 13 to a low of 9.0 ppm on July 11 with a mean summer value of 14.0 ppm (Table II). Secchi disk measurements made bi-monthly averaged 3.2 ft (0.98 m) and at no time was the bottom of lower Big Creek visible from the surface.

The mean turbidity values for the major Bay Stations (D–K) varied between 3.0 and 5.9 ppm with a mean summer value of 4.3 ppm (Table II). Bi-monthly Secchi disk readings showed the bottom of the Bay to be visible at the time when over 66% of the observations were made. However, at no time was the entire bottom of the Bay obscured by the turbidity of the water. Summer Secchi disk values for the days when the bottom was not locally visible, ranged between 4 and 9 ft, and averaged 6.4 ft (1.95 m).

Levels of turbidity were much higher in Big Creek than in the waters of Inner Long Point Bay. The bi-weekly turbidity determinations in Big Creek showed peaks in early June and early September associated with freshets caused by 1.81 and 0.1 inches (4.6 and 0.3 cm) of rainfall, respectively. Fluctuations in the mean bi-monthly average turbidity levels for all major Bay Stations were much less extreme, varying only 30% from the seasonai mean in contrast to 100% in the waters of Big Creek. Average turbidity levels

TABLE II. Comparative bimonthly physical and chemical data for lower Big Creek and Inner Long Point Bay for the period of May 30–September 6, 1962. Levels for the Creek represent averages for Stations A and B. Levels for the Bay represent averages for Stations D, E, F, G, I, J, K. Levels are expressed in ppm.

	May 30		June 13		June 27		July 11		July 26		Aug. 9		Aug. 22		Sept. 6		Seasonal average	
	Creek	Bay	Creek	Bay	Creek	Bay	Creek	Bay	Creek	Bay	Creek	Bay	Creek	Bay	Creek	Bay	Creek	Bay
Total Solids	326	202	293	180	267	145	329	166	323	157	306	150	353	185	327	195	315.5	172.5
Turbidity	11.3	5.9	26.0	5.2	11.0	3.0	9.0	3.7	–	–	10.8	4.0	10.0	3.9	20.0	4.1	14.0	4.3
*p*H	–	–	–	–	8.1	8.1	8.2	8.3	–	–	–	–	8.3	9.0	8.5	8.8	8.2	8.6
Phosphate	0.18	0.06	0.19	0.06	0.19	0.08	0.13	0.05	0.16	0.06	0.13	0.09	0.16	0.07	0.20	0.09	0.17	0.07
Free ammonia	–	–	0.06	0.12	0.13	0.15	0.07	0.03	0.08	0.07	0.06	0.10	0.16	0.08	0.16	0.11	0.10	0.09
Nitrates	–	–	0.40	0	0.30	0	0.08	0	0.25	0	0.20	0	0.25	0	0.10	0	0.23	0
Nitrites	–	–	0.01	0	TR	0	TR	0	TR	0	0	0	0.01	TR	0.01	0	0.06	TR
Total alkalinity	–	–	–	–	180	86	165	59	170	61	175	66	182	65	177	64	174.8	66.8
B.O.D.	1.3	1.8	3.2	2.4	1.4	1.0	2.0	1.0	0.8	0.9	1.1	0.9	1.4	1.4	1.0	1.4	1.5	1.4

in the Bay, therefore, are much less affected by run-off than those in Big Creek and the fluctuations in average Bay turbidity show no significant correlation with those of the Creek ($r = 0.21$).

A comparison of average summer turbidity levels for individual Stations, plotted in Fig. 5, showed a progressive decline in turbidity from Big Creek (Stations A and B) to a low of 2.6 ppm towards the middle of the Bay at a distance of approximately 15,000–20,000 ft (4600–6098 m) from the Creek mouth (Stations E–I). The turbidity decreased rapidly through the estuary (Station C) to Station D, some 10,000 ft (3049 m) from the Creek mouth. A slight but gradual increase in turbidity levels occurred from the mid-Bay Stations towards the opening into Lake Erie, i.e. through Stations G and H.

It is apparent that Big Creek waters carry consistently a load of suspended materials into Inner Long Point Bay. The marked decline in Bay turbidity levels within the first 10,000 ft (3049 m) of the Creek mouth, and the general clarity of Bay water at the more remote Stations, indicates that the major influence of the Creek on Bay turbidities during the summer months is restricted to the area adjacent to the Creek mouth where the suspended material is largely precipitated. This observation is confirmed by extensive deposits of silt in that area of the Bay.

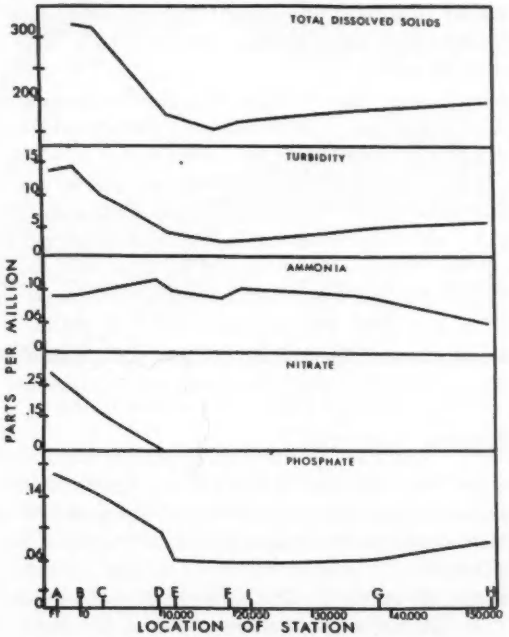

FIG. 5. Summer levels of total dissolved solids, turbidity, free ammonia, nitrate, and phosphate for major stations on Big Creek and Inner Long Point Bay for the period of May 30–September 6, 1962.

PHOSPHATE

Phosphate levels for the water of Big Creek were considerably higher than for that of Inner Long Point Bay (Table II). Summer phosphate levels in Big Creek averaged 0.17 ppm and fluctuated between 0.13 and 0.20 ppm. No seasonal trend in phosphate levels was evident for the Creek water. However, a slight seasonal trend in phosphate levels occurred in the Bay water (average of Stations D–H), increasing from 0.06 ppm in late June to 0.09 ppm in mid August and early September.

Highest phosphate levels were recorded at Station A of Big Creek. An analysis of average seasonal phosphate values for the major Creek and Bay Stations (A–H), shown in Fig. 5, revealed a marked decline in Big Creek between Stations A and B (over a distance of 3000 ft or 915 m) a further reduction at estuarial Station C, and a continuation of the pronounced decline to Station E, about 12,000 ft (3659 m) from the Creek mouth.

Soil phosphate levels of bottom samples taken at the Creek Stations and at 7 major and 10 minor Bay Stations are presented in Table IV. Soil phosphate levels in the Creek, averaging 53.5 ppm, showed a progressive increase from Station A (11.0 ppm) to Station C (89.5 ppm). Soil phosphate levels in the Bay Stations averaged 37.3 ppm. Relatively high phosphate levels exceeding 100 ppm were found at several of the Bay Stations extending from the mouth of Big Creek through a narrow zone towards Lake Erie. This zone of high soil phosphate levels is shown in Fig. 6.

This observed increase in soil phosphate levels through lower Big Creek, its estuary, and adjacent Bay (Stations A–E) correlated negatively with the decrease in the levels of phosphate in the Creek water ($r = 0.84$) over the same distance, suggesting a major settling out of the phosphates carried by the Creek water. It would seem improbable that the observed reduction in phosphate levels in the Creek water was caused by a significant absorption of this nutrient by aquatic vegetation because the turbidity of the Creek water was too great to permit much photosynthesis by aquatic vegetation. However, the relatively high levels of phosphate in the Bay sediment adjacent to the Creek mouth may be the result of the deposits of previously absorbed phosphates by decaying vegetation.

NITRITE AND NITRATE NITROGEN

Nitrite nitrogen was typically present in the water of Big Creek in trace amounts, but not exceeding 0.01 ppm during the summer of 1962 (Table II). Traces of nitrite nitrogen were detected in Inner Long Point Bay only on August 22 at Station K.

Nitrate nitrogen occurred in all Creek water samples taken during the summer (Table II). The mean seasonal nitrate level for Big Creek (average of Stations A and B) was 0.23 ppm. The maximum level of 0.40 ppm was recorded on June 13 coinciding with freshet conditions which resulted, also, in the highest turbidity recorded during the summer. The nitrate level declined to 0.08 ppm

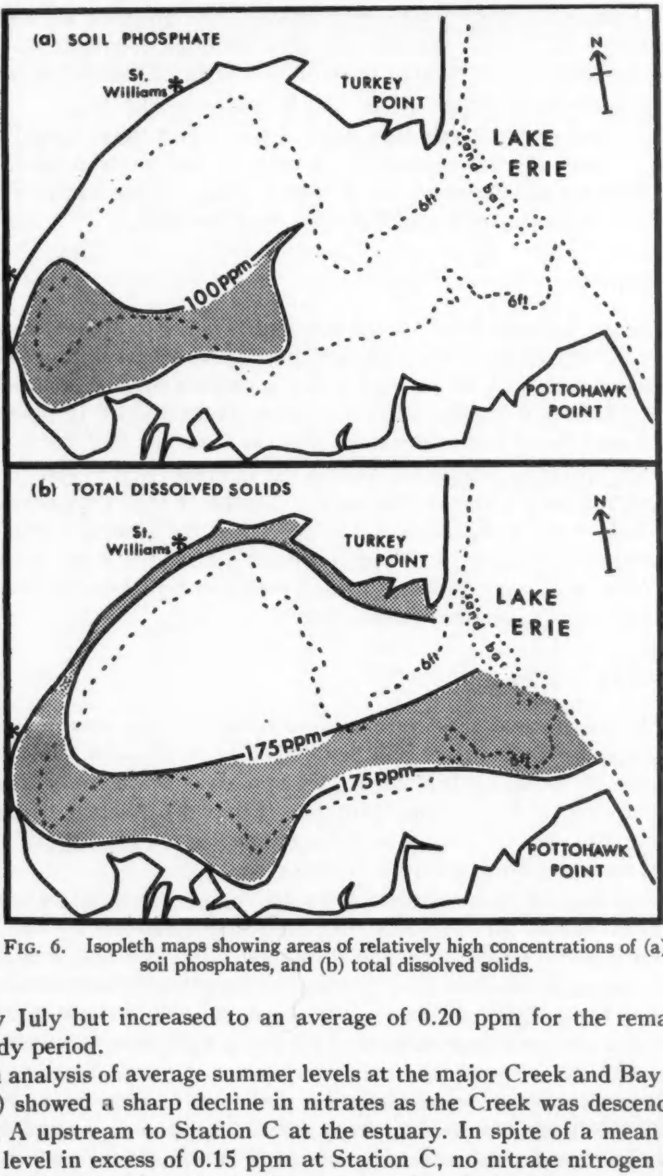
(a) SOIL PHOSPHATE
St. Williams
TURKEY POINT
LAKE ERIE
N
sand bar
6ft
100ppm
6ft
POTTOHAWK POINT
(b) TOTAL DISSOLVED SOLIDS
St. Williams
TURKEY POINT
LAKE ERIE
N
sand bar
6ft
175ppm
175ppm
6ft
POTTOHAWK POINT

FIG. 6. Isopleth maps showing areas of relatively high concentrations of (a) soil phosphates, and (b) total dissolved solids.

in early July but increased to an average of 0.20 ppm for the remainder of the study period.

An analysis of average summer levels at the major Creek and Bay Stations (Fig. 5) showed a sharp decline in nitrates as the Creek was descended from Station A upstream to Station C at the estuary. In spite of a mean seasonal nitrate level in excess of 0.15 ppm at Station C, no nitrate nitrogen could be detected at any of the Bay Stations at any time during the summer months.

It is probable that the absence of detectable levels of nitrate nitrogen in the Bay may be related to the utilization of nutrients by aquatic plants which cover much of the bottom of the Bay. Some 50% of the decline in nitrate levels (between Stations A and C) occurred where rooted aquatics are confined to the margins of the Creek, because of high turbidities, low light penetration, and possibly other factors. Similar reductions in nitrate levels by aquatics have been reported by Kleerekoper (1944) and Hutchinson (1957).

Data on soil nitrate levels for lower Big Creek and Inner Long Point Bay are given in Table IV. The respective mean soil nitrate levels in the Creek and the Bay were 8.0 (7.5–9.0) and 8.3 (6.0–10.5) ppm. No pattern of differences in the level of soil nitrates through the Bay was observed.

Free Ammonia

The mean summer level of ammonia nitrogen was approximately 0.10 ppm for both Big Creek and Inner Long Point Bay. Creek levels ranged between a minimum of 0.06 ppm on June 13 and a maximum of 0.16 ppm on August 22; Bay levels from 0.03 ppm on July 11 to a maximum of 0.15 ppm on June 27. No seasonal trend was evident in either the Creek or Bay water.

Average ammonia nitrogen levels for the summer (Fig. 5) were similar at all Stations, reaching a low of 0.06 ppm at Station H near the opening of the Bay into Lake Erie, and a high of 0.11 ppm near the village of Port Rowan where the highest value of 0.19 ppm recorded during the study occurred on June 27. Ammonia levels recorded in the Creek and Bay were below the level indicative of organic pollution (Klein, 1959).

Total Dissolved Solids

The levels of total dissolved solids recorded at the major and minor study Stations between June 7 and September 3 are given in Table III. The average seasonal value for Big Creek (324 ppm) was nearly twice as great as that for the water of Inner Long Point Bay (178 ppm). Average Creek values varied from 305 ppm on July 5 to 333 ppm on August 14; Bay values from 170 to 203 ppm on July 5 and June 7, respectively.

A comparison of the total dissolved solids values at the major and minor Bay Stations (Table III), revealed consistent differences among the various Bay locations, some Stations having values typically higher than others. Using data from the major Stations (B–H), it was evident (Fig. 5) that water flowing into the Bay from Big Creek was high in dissolved solids but, on entering the Bay, the value decreased approximately 50% through a distance of 10,000–12,000 ft (3049–3659 m) between the estuary (Station C) and Stations D and E. The average seasonal value reached a minimum at Stations E, F, and I (12,000–22,000 ft or 3659–6707 m from the Creek estuary) beyond which it increased slightly towards Station H, some 53,000 ft (16,158 m) from the Creek mouth and near the opening between the Bay and Lake Erie. The increase in values at Stations G and H is attributed to the mixing of the water of the Inner Bay with that of the Outer Bay (Lake Erie) which was reported by Rodgers (1960) to have a total dissolved solids value of about 200 ppm.

TABLE III. Total dissolved solids values for two Stations on Big Creek and 25 Stations on Inner Long Point Bay. Levels are expressed in ppm.

Station	June 7	June 25	July 5	July 29	Aug. 3	Aug. 14	Aug. 21	Sept. 3	Seasonal average
Creek									
B	324	335	280	325	335	345	340	315	324.9
C	333	320	330	320	310	320	315	325	322.6
Average:	328.5	327.5	305.0	322.5	322.5	332.5	327.5	320.0	323.7
Bay									
D	245	215	233	178	167	188	185	186	199.6
E	186	165	168	198	165	179	175	156	174.0
F	180	155	140	150	160	165	158	163	158.9
G	–	165	175	170	183	192	192	173	178.6
H	–	210	165	165	220	208	218	169	193.6
I	185	147	158	142	175	188	195	180	171.2
J	237	180	–	168	168	170	170	177	181.4
K	215	165	165	165	168	172	168	185	175.4
Ia	165	182	175	170	150	180	205	210	179.0
Ib	165	165	148	223	150	190	175	155	171.3
Ic	205	200	235	210	215	230	200	158	206.6
IIa	210	180	180	182	150	165	170	180	177.1
IIb	210	140	160	140	165	185	180	165	168.1
IIc	217	157	160	160	160	165	168	170	169.6
IId	212	150	150	150	157	166	174	175	166.8
IIe	212	–	145	168	166	165	158	162	168.0
IIf	202	145	145	152	150	157	157	172	160.0
IIg	–	–	180	163	168	158	193	185	174.5
IIIa	200	155	180	143	160	190	175	155	169.8
IIIb	190	200	148	155	155	170	190	135	167.9
IIIc	210	160	155	170	158	190	212	158	176.6
IIId	–	210	190	215	215	210	218	170	204.0
IIIe	–	180	210	205	218	205	215	180	210.9
IIIf	–	200	170	200	187	190	183	142	181.7
IIIg	–	170	145	172	153	168	166	138	158.9
Average:	202.6	173.7	170.0	172.6	171.3	181.4	184.0	167.9	177.4

The persistent differences in the value of the total dissolved solids recorded among the 25 individual major and minor Stations during the eight scheduled samplings of the Bay water permitted the construction of isopleths by which relative values of dissolved solids occurring through the Bay were compared. By this method, higher values of total dissolved solids were found to occur within a specific area than elsewhere in the Bay during each of the bi-monthly surveys.

Arbitrarily using the 175 ppm isopleth to define the area of higher total dissolved solids, it was possible to describe the path of the discharge from Big Creek through Inner Long Point Bay to Lake Erie. Employing the mean summer data for 1962, it may be seen (Fig. 6) that higher values of dissolved solids occurred over an area extending from the mouth of Big Creek eastward in a relatively narrow band through the deeper part of the Inner Bay to the channels through the Pottohawk–Turkey Point sand bar linking Inner Long

TABLE IV. Analysis of bottom soil samples collected from Big Creek and Inner Long Point Bay Stations, June 19, 1962.

Station	Soil texture	*p*H	Nitrate (ppm)	Phosphate (ppm)	Potash (ppm)	Magnesium (ppm)
Creek						
A	Sand	7.4	9.0	11.0	32.0	50.0
B	Silt loam	7.5	7.5	60.0	39.0	50.0
C	"	7.5	7.5	89.5	47.5	50.0
Average:		7.5	8.0	53.5	39.5	50.0
Bay						
D	Silt loam	7.6	10.5	86.0	45.0	50.0
E	"	7.5	9.0	104.5	61.0	50.0
F	"	7.6	9.0	26.0	35.0	125.0
G	"	7.5	7.5	15.0	61.0	125.0
I	"	7.4	6.0	30.0	51.5	125.0
J	"	7.7	7.5	19.0	37.0	125.0
K	"	7.5	6.0	15.0	56.5	125.0
Ic	"	7.5	9.0	60.0	42.0	50.0
IIa	"	7.3	10.5	82.0	47.5	50.0
IIb	"	7.4	7.5	19.0	42.0	50.0
IIc	Sand	7.5	7.5	15.0	50.5	50.0
IId	Silt	7.6	9.0	60.0	41.5	50.0
IIe	Silt loam	7.7	7.5	15.0	24.0	125.0
IIf	"	7.4	7.5	19.0	45.0	125.0
IIIa	"	7.3	6.0	34.0	54.5	125.0
IIIb	"	7.3	7.5	15.0	29.0	125.0
IIIc	"	7.5	9.0	19.0	61.0	125.0
Average:		7.5	8.3	37.3	46.1	94.1

Point Bay with Lake Erie. A narrow arm joining St. Williams and Port Rowan with the area near the mouth of Big Creek would seem to represent the influence of effluents from these two municipalities.

BIOCHEMICAL OXYGEN DEMAND

B.O.D. levels (Table II) were similar at all Big Creek Stations with a seasonal average of 1.5 ppm. Seasonal variations were modest ranging between 0.9 and 3.2 ppm. The seasonal average of all Bay Stations was also 1.5 ppm. Levels at the various Bay locations ranged from a low of 0.6 to a high of 3.0 ppm. No significant differences were observed in B.O.D. levels among the Bay Stations.

The levels of B.O.D. recorded for the Creek and Bay water during the summer of 1962 was within the range indicative of unpolluted waters according to the classification of the Royal Commission on Sewage Disposal (1912).

SUMMARY AND DISCUSSION

A study was carried out in 1962 to document and compare the summer limnological conditions of lower Big Creek and Inner Long Point Bay of Lake

Erie, including an appraisal of the effect which the Big Creek drainage may have on water conditions within the Inner Bay.

The mean water level of Inner Long Point Bay, varying 0.8 ft (0.24 m) during the summer months, was controlled by that of Lake Erie. Summer variations in the flow of Big Creek had no apparent influence on the mean water level within the Bay. Observed short-term fluctuations in the water levels of the Bay were caused by seiche action resulting in a maximum vertical displacement of 1.53 ft (0.46 m) and a mean period between peaks of 13.3 hr. Seiches recorded for Inner Long Point Bay were similar to those described for Lake Erie in terms of amplitude, period, and duration.

A significant correlation between the water temperatures of the Creek and the Inner Bay ($r = 0.78$) was caused by the response of each to ambient air temperatures. However, the correlation of mean air temperature with the water temperature of Big Creek ($r = 0.66$) was lower than that with the Bay water ($r = 0.89$) and accounted for a more stable and less extreme summer water temperature in the Creek than in the Bay.

The waters of both Big Creek and the Inner Bay were alkaline, *p*H values of both reaching a seasonal maximum in late August. That of the Creek water reached a maximum of 8.5, that of the Bay water 9.0. Total alkalinity levels at any given time were two to three times higher in Big Creek (165–182 ppm) than in Inner Long Point Bay (59–86 ppm).

Turbidity levels in Big Creek were consistently two-to-five-fold higher than in Inner Long Point Bay and subject to much wider fluctuations (9.0–26.0 ppm) than the Bay water (3.0–5.9 ppm). The sharp reduction in the turbidity of the Bay water within about the first 10,000 ft (3049 m) of the Creek mouth resulted from the precipitation of suspended materials carried by Big Creek, and caused an obvious deposition of sand, silt, and muck over an extensive area of the bottom.

The mean seasonal level of total dissolved solids recorded for Big Creek was nearly twice that for the Inner Bay, the level decreasing abruptly in the Bay within a distance of approximately 15,000 ft (4573 m) of the Creek mouth from 232 to about 175 ppm. An analysis of differences in local levels of dissolved solids recorded at the Bay Stations, expressed isoplethically, isolated an area characterized by levels of dissolved solids exceeding 175 ppm which linked Big Creek with Lake Erie. The use of total dissolved solids is advocated as a simple but effective method for tracing the movement of the discharge from Big Creek through the waters of Inner Long Point Bay to Lake Erie.

Phosphate levels in Big Creek (0.13–0.20 ppm) were typically two to three times higher than in the Bay (0.06–0.09) at any one time. Nitrate nitrogen occurred regularly in the Creek water with a mean summer value of 0.23 ppm (0.08–0.40 ppm) but could not be detected in the Bay beyond the estuary at any time. Trace amounts of nitrite nitrogen occurred regularly in the Creek water but were not recorded at any of the Bay Stations. The phosphate and nitrate levels showed a similar steady decline through lower Big Creek, its estuary, and the adjacent Bay, reaching their lowest levels at a distance of about 10,000 ft (3049 m) from the Creek mouth. This negative trend was apparent, also, for turbidity levels and suggested the possibility that available phosphates and nitrates may have been precipitated along with the suspended solids carried by the Creek water.

The phosphate levels of soil samples taken from the bottom of the Creek and Bay showed a significant inverse correlation ($r = 0.84$) with water phosphate levels over the same distance (Stations A–E) indicating that much of the phosphate carried towards the Bay by the Creek water was deposited in the lower part of the Creek and its estuary. Comparatively high levels of soil phosphates occurred in that part of the Bay through which the path of the Creek discharge to Lake Erie was traced by the levels of total dissolved solids. Levels of soil potash showed a similar increase in the Creek between Station A (32.0 ppm) and C (47.5 ppm) but levels were relatively uniform through the bottom of the Bay, averaging 46.1 ppm.

Soil nitrate levels were characteristically low in the bottom samples taken from the Creek and Bay (8.0 and 8.3 ppm, respectively) and showed no differences to conform with the spectacular decrease in nitrate levels of the Big Creek discharge between Stations A and D. Because of the high turbidity limiting photosynthesis, it seemed improbable that the loss of nitrate from the water of lower Big Creek could be explained by its utilization by aquatic plants. However, the low level of nitrates in bottom samples taken from the Bay, coupled with a failure to detect the presence of nitrates in the Bay water, suggested that available nitrogen may be more-or-less fully utilized by the luxuriant aquatic vegetation growing in Inner Long Point Bay during the summer months.

Mean summer values of free ammonia (0.10 ppm) and biochemical oxygen demand (1.5 ppm) were similar for the waters of Big Creek and Inner Long Point Bay. No significant seasonal trend was recorded in either case, nor was there a notable difference in values from the various Creek and Bay Stations. The mean summer values for the Creek and Bay were within a range considered to be indicative of waters free of organic pollution.

It is concluded from this study that the continuous contribution of nutrients and suspended materials from Big Creek is an important factor in the ecological aging of the Bay. However, it would seem that the existence of the channels through the sand bar across the Bay mouth which are necessary for the interchange of water between the Bay and Lake Erie and the access of important spawning migrations of fishes to the Big Creek drainage system is dependent on the combined scouring action of the Creek discharge and Lake Erie seiches.

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Influence of Temperature, Salinity, and Photoperiod on the Aggregations of Chum Salmon Fry (*Oncorhynchus keta*)[1,2]

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ABSTRACT

Underyearling chum fry from hatchery stock were held in fresh water and salt water at two different temperatures and under two different photoperiods and acclimated to these conditions for 40 days before testing started. Aggregations were greater in salt water than in fresh water ($p < .01$). Fish acclimated to cold water schooled more strongly than those acclimated to warm water but this effect was not considered statistically significant. There were no differences in intensity of aggregation due to photoperiod ($p > .05$). The significance of these findings is discussed in relation to life history of the fry.

INTRODUCTION

THERE ARE conflicting reports on the schooling behaviour of migrating salmon fry. Hoar (1953) described the downstream migration of shoals of chum salmon (*Oncorhynchus keta*) as a displacement resulting from the failure of the rheotactic response in a period of night blindness. McDonald (1960) reported that schools of chum fry were seen at the mouth of the Lakelse River and in the quiet waters of the Skeena River. He did not observe any schools of these fish in the streams from which they migrated.

Observations of migrating pink fry (*O. gorbuscha*) in nature suggested that these fish were hidden under stones during the day but migrated actively and individually downstream at night (Neave, 1955). In slack (tidal) water these pink fry were swimming randomly and were more uniformly distributed (it is not clear whether they were schooled here or not). Hoar (1956) found that actively migrating pink fry captured at night were not schooled until after a period of exposure to light. Exposure for 15 min under artificial light was sufficient to ensure that nonschooled migrants would be schooled when returned to the river the next day. Hoar thought that this change depended on some very rapid type of learning. The individual fish which Neave had reported would probably take cover in the stones the next day, while the fish which had schooled would remain grouped.

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In addition, Hoar (1956) thought that behavioural changes in underyearling fry might be correlated with the length of time they have been held in captivity. The fry studied by Hoar prior to 1956 had sometimes been held beyond the end of the normal migration period; thus, the behaviour described might not have been that of migrating salmon. In this connection, McInerney (MS, 1961) recorded changes in the size of groups of chum fry as they swam over a partition in a salinity preference tank. The size of such groups was maximal in July, with smaller aggregations preceding and following that time. This indicates that schooling was most intense in July.

From this brief review, it appears that the schooling reactions of salmon fry vary at definite times. Both of the schooling migrant fry (chum and pink) have been described as nonschooling at the start of their migration, yet a schooling reaction can take place before they reach the ocean. Since schooling appears consistently at some stage in migrating pink and chum salmon fry it is assumed that this is an integral part of their migratory behaviour.

As a further contribution to the analysis of schooling in migratory fry, the aggregative behaviour of hatchery-reared underyearling chums has been studied at the time of the maximal schooling tendency shown by McInerney (MS, 1961). In July 1964 the effects of salinity, photoperiod, and temperature were examined in order to discover any possible environmental effects on schooling behaviour.

MATERIALS AND METHODS

Holding Conditions

Chum fry approximately 6 weeks post-hatching were obtained from the Smith Falls Hatchery, Cultus Lake, on April 17, 1964. They were held in four tanks with temperature and photoperiod controlled as follows: Tank A was at 9–12 C with an 8-hr day; B was at 9–12 C with a 16–17.5-hr day; C was at 7 C with a 16–17.5-hr day, and D was at 7 C with an 8-hr day. The 9–12 C range and the 16–17.5-hr range depended on seasonal fluctuations. The 7 C level and the 8-hr period were maintained accurately. The fish were fed three times daily with fresh-frozen brine shrimp (*Artemia*).

On May 21, some of the fish under each of these conditions were transferred to four saltwater tanks under the same temperature and photoperiod regime as the freshwater ones. The salinity of this salt water varied from 25 to 29‰. Testing commenced on June 30, 40 days after this transfer to the seawater tanks.

The freshwater tanks held 202 liters of water and 1500 fish with a resulting density of 7.4 fish/liter. The saltwater tanks held 67 liters of water and 250 fish; here the density was 3.7 fish/liter. Two factors governed the optimum number of fish that could be maintained in the freshwater and seawater tanks: first, the oxygen-carrying capacity of fresh water is greater than that of salt water and hence relatively more fish could be maintained in the fresh water. Second, the water in the freshwater tanks was flowing slowly through the tanks at all times while the water in the saltwater tanks was not flowing but was changed twice a week. Both freshwater and saltwater tanks were aerated.

The smaller size of the saltwater tanks and/or the difference in density might have had an effect on behaviour which would have obscured any true effect of salinity. Moreover, the smaller number of saltwater fish would be resampled more frequently than the freshwater ones. As a control for these situations, a special test on freshwater fish was carried out in November following the main experiments. For this, 250 freshwater fish were placed in fresh water in one of the smaller tanks. They were acclimated for 29 days before testing and compared with fish from a larger tank. An analysis of variance on the data collected using the standard aggregation test described below provided an F value of less than unity. That is to say, the schooling behaviour of these fish was not significantly different at the 5% level from the main freshwater population after 29 days of conditioning to the small tank. Since the differences in size and density between the two tanks was not shown to affect behaviour, any salinity effect will be assumed valid.

Testing Apparatus

To measure the aggregating tendency, a series of four testing tanks was designed so that the fish could be isolated from one another until it was wished to allow them free movement. When released, they were free to swim individually around the apparatus until they made contact with one another. An observer could record the distribution of fish at certain times and thereby obtain a numerical record of the schooling tendency.

The four circular tanks (Fig. 1) were partitioned internally by six double walls which ran radially from the central drain pipe. Each tank was cooled by a water bath to the seasonal level (9–12 C) and was screened from neighbouring tanks.

Sliding doors were hung between the double walls, permitting the fish to move out of its own sector and around the apparatus when the doors were opened. The doorways were placed at the inner and outer ends of the partitions, alternately, as shown in Fig. 1. This design was adopted to prevent the constant circling behaviour of chum fry described by Hoar (1956). The doors were drawn aside by a system of cords and pulleys while the observer remained concealed behind a screen. The fish were observed from above with the use of a mirror inclined at approximately 45° above the tank.

Light was provided by vertical 40-w fluorescent tubes, each 30 cm long, which were supported on the screening round the tank at the ends of the double walls. The lower end of each tube was about 5 cm above the top of the tank. This arrangement of lights enabled the observer to see the fish well-illuminated without being dazzled by any surface reflection and provided uniform lighting for the tank.

The fish were never fed in the testing tanks. There was no externally-induced water current in the tanks during testing.

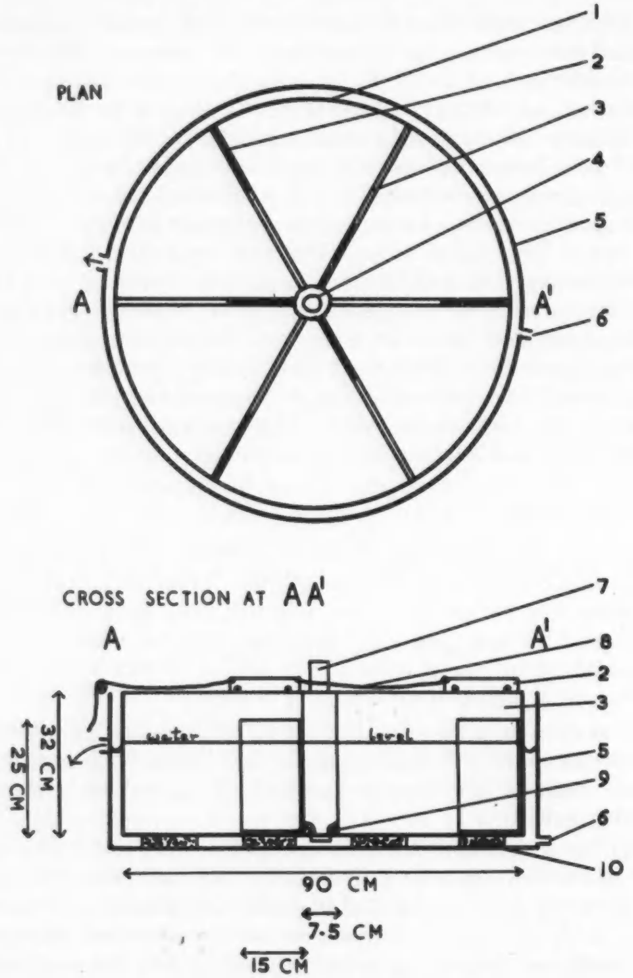

FIG. 1. The testing tank: 1, outer wall of testing tank; 2, door which can be lifted by draw-string shown at 8; 3, partition which is double-walled and supports door; 4, position of drain with its plug shown in position (section AA') at 7 and the drainage holes from the compartments at 9; 5, wall of outer cooling bath with the inlet for cooling water at 6 and the outlet shown at the arrow; 10, supports on which the testing tank rests on the bottom of the cooling tank. Description of apparatus in text.

TESTING TECHNIQUE

Six fish were placed in the testing tank, one in each sector, with the doors closed. They were left undisturbed for a period of 1 hr. The doors were then opened slowly. This movement, no matter how carefully executed, generally startled one or more fish for a few minutes. Hence, their positions were not recorded for a further 10 min. The test consisted of 30 observations 20 sec apart in a 10-min period. The number of fish in each sector was recorded at each observation. At the end of the test the number of groups of the same size was totalled; later, certain selected tests were re-scored with a chi-square value based on the distribution pattern at each observation. The scoring is explained in detail below.

Occasionally, a fish might become "excited" by the opening of the doors and dash round the tank, disturbing the others. Such data were considered abnormal and are not included. This event occurred rarely, and generally when a particularly small fish ("pinhead") was accidentally placed in the tank. The rarity was due to the careful selection of fish of the same size for testing. "Pinheads" or exceptionally large fish were not placed in the testing tanks after the nature of this disturbance was appreciated.

The full test took about 1 hr for all four testing tanks. It was just possible to run three full tests each day within the time limit set by the 8-hr photoperiod of the short-day fish. At the end of the day, the tanks were cleaned, drained, and refilled with fresh or salt water as appropriate. This water was oxygenated during the night; next day, the airstones were removed before any fish were put in the tank.

RESULTS

GROSS DATA

Totals of data for all the tests are presented in Table I, which shows the frequency of group-size multiplied by the size of that particular group. For

TABLE I. Gross totals for all tests (description in text).

No. of tests[a]	Tank salinity[b]		Group freq. × Group size		Groups 4–6 as per cent	Groups 4–6 as per cent total for temperatures and photoperiods	
			1–3	4–6			
26	A	FW	3368	1312	28.0		
24		SW	1906	2414	55.9	*Temperatures*	
24	B	FW	2918	1402	32.5	High	41.7%
22		SW	1959	2001	50.5	Low	48.9%
28	C	FW	3461	1579	31.3		
23		SW	1498	2642	63.9	*Photoperiods*	
28	D	FW	3024	2016	40.0	Long	44.5%
25		SW	1787	2713	60.2	Short	46.1%

[a] One test consists of 30 observations over a 10-min period.

[b] For details on tank treatments A, B, C, and D see Materials and Methods; FW = freshwater, SW = saltwater.

example, if 20 groups of size 2 (i.e. two fish recorded in a certain sector 20 times during the 10-min test) occurred in a test, the score of 20 × 2 = 40 would be entered into the total of the 1–3 groups column in Table I. Thus, the totals show the number of fish participating in any one group-size. Groups of sizes 1–3 are totalled and presented as a contrast to the totals of sizes 4–6, the stronger aggregations. This 4–6 groups total is also presented as a percentage of the whole to indicate the trends in these gross data (from which the samples were taken later). The effects of salt water vs. fresh water can be judged from the right-hand column of Table I. The percentages for the temperature and photoperiod effects are also shown.

These data were used as the basis for an analysis of variance, using the randomized blocks design (Snedecor, 1959). Only the results from one freshwater and one saltwater testing tank were used for the analysis data. This was to allow for the occasional test which was rejected because of abnormalities in behaviour. These were selected randomly from the two freshwater and two saltwater tanks used in each trial. To obtain a single index of aggregation, the tests were re-scored as follows.

Each of the thirty distributions of fish in the 10-min test was re-scored with a chi-square value based on 1:1:1:1:1:1 as the hypothetical distribution for nonaggregated fish. These chi-square values are given in Table II. Each test of thirty chi-square values was summed and the resulting number was named the "aggregation index." This index provided the raw data for the analysis of variance.

TABLE II. Chi-square values for each distribution pattern in the testing tank ranging from complete uniformity of one fish in each compartment (111111) to a situation of all six fish in one compartment (000006)

Distribution of fish in the six sectors	χ^2	Schooling tendency
000006	30	Strong
000015	20	
000024	14	
000033	12	
000114	12	
000123	8	
000222	6	
001113	6	
001122	4	
011112	2	
111111	0	Weak

It was possible to use three replications of each holding tank (treatment) within each of four time units (blocks). The blocks covered a period of 4–5 days and their dates are as follows: July 4–9, block 1; July 16–20, block 2; July 21–24, block 3; July 27–31, block 4.

The experiments were run for less than 1 month and since the record of seasonal change in chum fry schooling recorded by McInerney (MS, 1961) shows little change over 1 month it was not expected that any seasonal changes would show during this period. This would seem to permit the consideration of time units as blocks in this analysis instead of assuming that time is a fourth treatment.

The totals for the different treatments are presented in terms of sums of the aggregation indices in Tables III–V. All possible interactions between the three different treatments and blocks were examined in the analysis of variance which is presented in Table VI.

Table VI shows the data treated as a model I analysis (Snedecor, 1959, p. 257). This model assumes that the block effects are fixed, i.e. that they are reproducible under the same conditions of sampling.

This attitude was permitted by the fact that these fish may have been conditioned to the apparatus by repeated sampling during the tests, even though

TABLE III. Temperature effects. Chi-square totals (aggregation index) for the four different time periods of the study (blocks) — further description in test.

		Blocks				
Tanks	Temperatures	1	2	3	4	Temperature totals
A and B	9–12 C	5700	4182	4484	4628	18,994
C and D	7 C	5108	6818	4949	4578	21,453
Block totals:		10808	11000	9433	9206	40,447

TABLE IV. Salinity effects. Chi-square totals (aggregation index) for the four different time periods (blocks) of the study — further description in text.

		Blocks				
Tanks	Salinities	1	2	3	4	Salinities totals
A, B, C, D	fresh water	3448	4986	3757	4336	16,527
A, B, C, D	salt water	7360	6014	5676	4870	23,920
Block totals:		10808	11000	9433	9206	40,447

TABLE V. Photoperiod effects. Chi-square totals (aggregation index) for the four different time periods of the study (blocks) — further description in text.

		Blocks				
Tanks	Photoperiods	1	2	3	4	Photoperiods totals
A and D	8 hr	5256	4919	4960	5310	20,445
B and C	16–17.5 hr	5552	6081	4473	3896	20,002
Block totals:		10808	11000	9433	9206	40,447

TABLE VI. Analysis of variance (model I of Snedecor, 1959; blocks as fixed effects).

Source of variation	Sums of squares	Degrees of freedom	Mean square	
Temperatures (T)	62,986	1	62,986	<.05
Salinities (S)	569,338	1	569,338	<.01
Photoperiods (P)	2,044	1	2,044	>.05
Blocks (B)	106,425	3	35,475	<.05
T × S	12,101	1	12,101	>.05
T × P	1,087	1	1,087	>.05
T × B	250,277	3	83,426	<.01
S × P	3,186	1	3,186	>.05
S × B	277,699	3	92,566	<.01
P × B	151,084	3	50,361	<.01
T × S × P	25,299	1	25,299	>.05
T × S × B	9,384	3	3,128	>.05
T × P × B	80,415	3	26,805	<.05
S × P × B	72,635	3	24,212	>.05
T × S × P × B	122,976	3	40,992	<.01
Residual	582,923	64	9,108	
Total:	2,329,859	95		

this effect may have been slight. A second consideration is the possibility of some seasonal change. If it were shown that the block effect was random a model II analysis would be appropriate. On the basis of these considerations the model I analysis was adopted.

Of the main effects, the aggregation index is significantly higher in salt water, at the 1% level. The index is significantly higher at the lower temperature than at the seasonal temperature, at the 5% level. Photoperiod effects are not significantly different. The main effect totals are presented in Tables III–V.

The significant blocks effect indicates that the aggregation indices summed over all three treatments differ significantly among the four blocks.

Since the primary interactions between the treatments do not show any significance at the 5% level, each treatment is operating independent of the others in the analysis. However, the treatments all interact individually with blocks. Interaction graphs of each main effect summed over the other two and then plotted for each block are presented in Fig. 2–4. Wherever the trend lines are not parallel an interaction is indicated. In addition, an approximation of the average slope of the four lines by eye will reflect the main effect. This is particularly noticeable in the photoperiod effect (Fig. 4) which is not significant. The average slope for the four blocks would approach the horizontal.

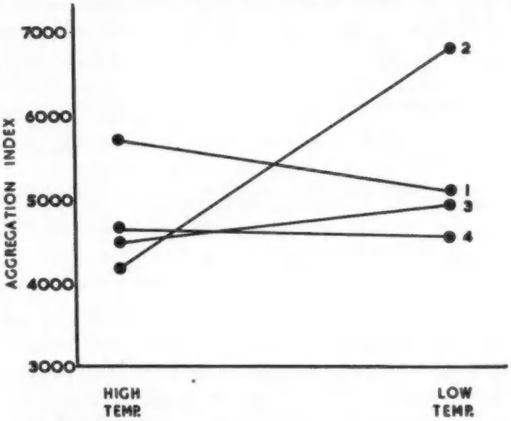

FIG. 2. Temperature effects as shown by plotting the aggregation indices for the four time period (blocks — Table III).

One other fact is apparent from these figures. It is not possible to point out one particular block as the cause of all the interactions. The situation is different for each main effect.

The three-way interactions are only significant in one instance, the T × P × B interaction. This is possibly due to the extremely large differences in the salinity effect of block 1 (Fig. 3). The salinity variation may also be responsible for the significance of the four-way interaction.

DISCUSSION

The experimental data show the highly significant effect of a saltwater environment in increasing the schooling tendency of these chum fry. Although

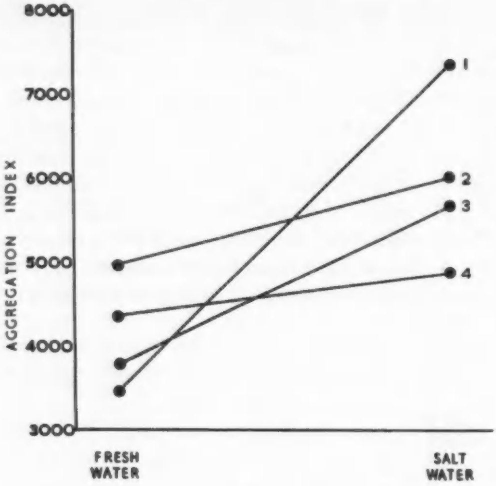

FIG. 3. Salinity effects as shown by plotting the aggregation indices for the four time periods (blocks — Table IV).

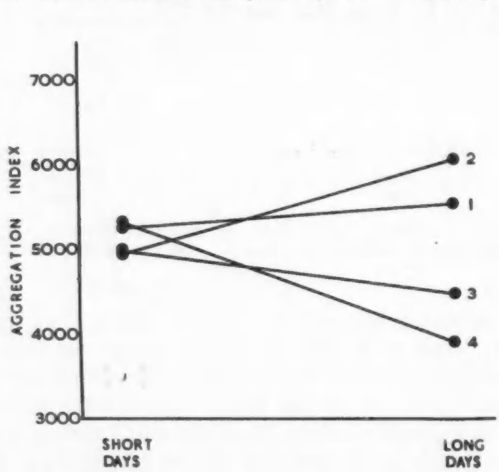

FIG. 4. Photoperiod effects as shown by plotting the aggregation indices for the four time periods (blocks — Table V).

the temperature effect also appears statistically significant, it is not considered biologically valid because both the 7 C and the 9–12 C fry were tested in water at 9–12 C. Temperature effects will not be discussed further.

It remains to consider the biological significance of the obvious response to salinity and the absence of response to photoperiod.

Photoperiod may be important as a triggering factor in timing the migration of salmon fry; it may also regulate the movements of these fish diurnally (Hoar, 1958). The seasonal cycle (emergence, schooling, onset of migration, etc.) may be hastened or delayed in salmon fry by artificial manipulation of the light–dark ratio. McInerney (MS, 1961) reported that a short photoperiod delayed the development of the "migratory behaviour complex" in coho yearlings, yet complete inhibition of this behaviour did not occur. In general, change in photoperiod may act as a stimulus to change in behaviour. It is not likely to act as a constantly directing factor in schooling.

Clearly, on the basis of these tests, stronger schooling occurs in salt water. Unless this is a laboratory artifact, it must have some meaning in the life history of chum fry. Many workers have described the schooling of juvenile salmon in fresh water. Schooling may be of little significance in migration per se (Hoar, 1956) but is more important as a means of escaping predators (Brock and Riffenburgh, 1960). It is in the marine habitat when the fish move away from landmarks that schooling has a distinct advantage. These salmon return to the natal streams at maturity; it may be more efficient biologically for a homing population of adult salmon to move in a group rather than individual fish. The adult salmon are often schooled in the ocean as is well known to fishermen who capture them in purse seines. Thus the effect of salt water in increasing the schooling tendency in the laboratory could also have a survival value for these fry in nature.

To find the physiological correlates of this behavioural change in salt water requires more experimentation. The effect may be correlated with a changed metabolism in salt water. Houston (1959) showed that chum fry would swim more slowly in salt water than in fresh water at maximum sustained speed. That study indicated that the loss of maintained swimming speed was due to the increased demand for energy to do osmotic work in the saltwater environment. If these fry do swim more slowly at normal speeds in salt water this might account for their greater aggregation since they might be less likely to lose one another. The general impression in this study, however, was that the saltwater fry were more active than the freshwater ones.

It is also possible to suggest an explanation in ethological terms. Increasing photoperiod and temperature allow the emergence of the fry from the gravel. The increasing photoperiod leads to greater activity and an ionic imbalance in chum fry, according to Eales (MS, 1963a; b). This is associated with increased thyroid activity which, in turn, must be triggered through the pituitary (Baggerman, 1960). Either the ionic imbalance or the direct pituitary effect may be considered the *stimulus* releasing *appetitive behaviour*. The appetitive behaviour is the increased activity, or "migration-disposition" of Baggerman (1960). The final result is the entry into salt water. In salt water either the increase expected in thyroid activity or some other factor acts to trigger the *consummatory behaviour*; this is the strong aggregative behaviour of the fry in salt water. If the change in the osmotic environment does trigger off a change in behaviour, it could be considered a releasing mechanism in the Lorenzian model of innate behaviour patterns (Tinbergen, 1951).

Further support for consideration of the saline environment as a part of the releasing mechanism for the strong schooling behaviour comes from Groot (personal communication). Groot placed underyearling chum fry in salt water and found a change in aggregation similar to that in the experiments described above. When Groot's fry were returned to fresh water the fry became less aggregated and more aggressive; that is, they return to their previous behaviour pattern. It appeared to Groot that the strong schooling in salt water could be switched on and off by the appropriate changes in environment.

Whatever the mechanism of this phenomenon or whatever physiological correlates can be found, it does appear to be real. The intense schooling in salt water is meaningful in terms of the life history of the fish; there is little reason to suppose that the event is only a laboratory artifact.

A fuller evaluation of the meaning of this saltwater effect would come from field studies on actively migrating fry. The apparatus described above would provide a measure of the schooling tendency. Chum fry could be trapped soon after emergence and at various times and locations during migration, as far downstream as the river estuary. Such an experiment would remove the obvious objections that can be raised against hatchery fish.

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NOTES

Northeastern Pacific Records of *Anoplogaster cornuta* Valenciennes (Anoplogasteridae: Pisces) and *Cyema atrum* Günther (Cyemidae: Pisces)

Since 1961 the Bureau of Commercial Fisheries, in cooperation with the U. S. Atomic Energy Commission, has been sampling the deep-water demersal fauna off the Washington and Oregon coasts. This note makes known two records of bathypelagic species, taken incidentally during the use of bottom sampling gear. A brief description of each species gives additional information on character variation.

Counts and measurements follow Hubbs and Lagler (1958) and were made from the left side except as explained in text. Radiographs were utilized for vertebrae and to check median fin ray counts. Total vertebrae include complete centra and the urostyle. The specimens were catalogued in the fish museum, University of Washington (abbreviated UW in text).

Anoplogaster cornuta Valenciennes, Fig. 1

Material: 1 specimen, male (?), standard length 109 mm (UW 16745).

Description: Measurements in terms of standard length: maximum depth 2.0; head 2.5; predorsal 2.2; preanal 1.3; snout to pectoral insertion 2.6; snout to pelvic insertion 2.1; length of dorsal base 2.5; length of anal base 9.9; width of pectoral base 14.5; width of pelvic base 27.3; longest dorsal ray 7.8; longest anal ray 10.4; longest pectoral ray 4.2; longest pelvic ray 5.7; length of gill opening 2.6; least depth of caudal peduncle 9.9. Measurements in terms of head length: orbit 5.7; interorbital width (at center of orbit) 3.4; length of snout 3.6; length of upper and lower jaws 1.3. Counts: D I, 18; A I, 8; P_1 16; P_2 I, 6; C V-21-V; branchiostegals 8; vertebrae 25; gill rakers 23 (including rudiments); pyloric caeca about 9 (partially decomposed).

Head and body covered with flattened, leaf-like ctenoid scales; each elevated above integument on pedunculate stalk. Head large (greater than $\frac{1}{3}$ standard length), deeply sculptured, with wide muciferous cavities, three naked membranous areas on cranium separated by bony bars or ridges. Suborbital bones enlarged, sculptured, possessing small erect spines. Postorbital articulating with the overlying preoperculum. Preoperculum without longitudinal sculpturing at downward and posterior angle (sculpturing evident on opercle). Opercle wider than preopercle, both displaying same angle in profile.

Mouth wide, subtending orbit; maxillary broadened at posterior end, and not entering gape. Cleft of mouth forming angle in head of about 70 degrees. Lower jaw broad; upper and lower portions striated, adjacent to a naked intermediate area. Upper jaw projecting beyond lower in closed position. Nondepressible teeth in both jaws long and strongly canine. Smaller teeth bordering entire outer ventral edge of premaxillary. Vomer and palatines edentulous. Basibranchial and lingual teeth present, similar in structure but smaller than those found on gill arches. Denticulated gill rakers ranging from a single cusp to a multifid tooth. Cephalic and preopercular spines reduced to slight protuberences.

Lateral line distinct and continuous, evenly arched, and developed as an open canal. Dorsal and anal single, with well-spaced, longitudinally sculptured rays; each ray decorated with short, laterally projecting spines. Color (in alcohol) uniform black throughout.

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Remarks: *Anoplogaster cornuta* undergoes marked metamorphosis. Juveniles bear little resemblance to adults; and as a result, the latter have been placed in *Caulolepis* as pointed out by Bertelsen and Grey (in Grey, 1955). By features outlined by Grey (1955), UW 16745 agrees fairly well with the adult (*Caulolepis*-form) of *A. cornuta.*

In comparison with the description of *Caulolepis longidens* Gill given by Goode and Bean (1896), UW 16745 displays some marked meristic differences. The type of *C. longidens* has a higher anal fin ray count, but this may be the result of counting the last fin ray as two instead of one. Goode and Bean (1896) also gave a high pelvic count (I, 7). Pelvic counts by Günther (1887) and Maul (1954) agree with UW 16745, as did counts given by Garman (1899) and Grey (personal communication). The present specimen has fewer vertebrae (25) than recorded by Garman (1899) but agrees with Günther (1887). Günther (1887) listed fewer pyloric caeca, but for smaller specimens (largest 77 mm).

Morphometrically, UW 16745 differs from the type of *C. longidens* in having: a longer head, less maximum body depth, a longer preanal distance, and a longer anal base (the last two measurements possibly a result of a strongly distended stomach). However, little faith can be placed on proportional differences in a species which shows such a marked allometric growth pattern.

Preliminary results from a world-wide study of the *Dana* collections of *Anoplogaster* intensify the relation between UW 16745 and *A. cornuta* (Grey, personal communication).

Distribution: Grey (1955) gives the recorded widespread, bathypelagic distribution of *A. cornuta* in the Atlantic from 44°N to about 46°S; and in the Pacific from the Gulf of Panama northward to off southern California, westward from Hawaii to the Bonin Islands. Pearcy (1964) listed this species from a mesopelagic survey off Oregon (Newport, Ore.; Pearcy, personal communication). UW 16745 slightly extends the known northward range limit in the eastern Pacific to off Tillamook Head, Oregon (45°56′N lat, 124°49′W long); it was taken from a 350-fath station, August 26, 1963.

The bathymetric range given by Grey (1955) for the adult *Caulolepis*-form is increased by the new record; the known range now is from 350 to 2678 fath. The young *Anoplogaster*-form occurs at more shallow depths, from 25 to 1685 fath (Grey, 1955).

Cyema atrum Günther, Fig. 2

Material: 1 specimen, female, standard length 122.2 mm (UW 17549).

Description: In accordance with Bertin (1937: 14): L 85.9Lt; H 11.0L; OR 9.0L; OM 6.4L; OP 17.0L; OD 61.0L; OA 61.4L; p 5.9L. Counts: D 87; A 81; P_1 13; total vertebrae 78 (27 caudal).

Remarks: Morphological variation for *C. atrum* is sufficiently documented (Bertin, 1937; Nybelin, 1948; Koefoed, 1955). The present specimen was in reasonably good condition except that the belly was split along the median abdominal line and the tip of the upper jaw was broken off at a point 2.6 mm behind the tip of the lower. Therefore, the length measurement (Lt) was taken

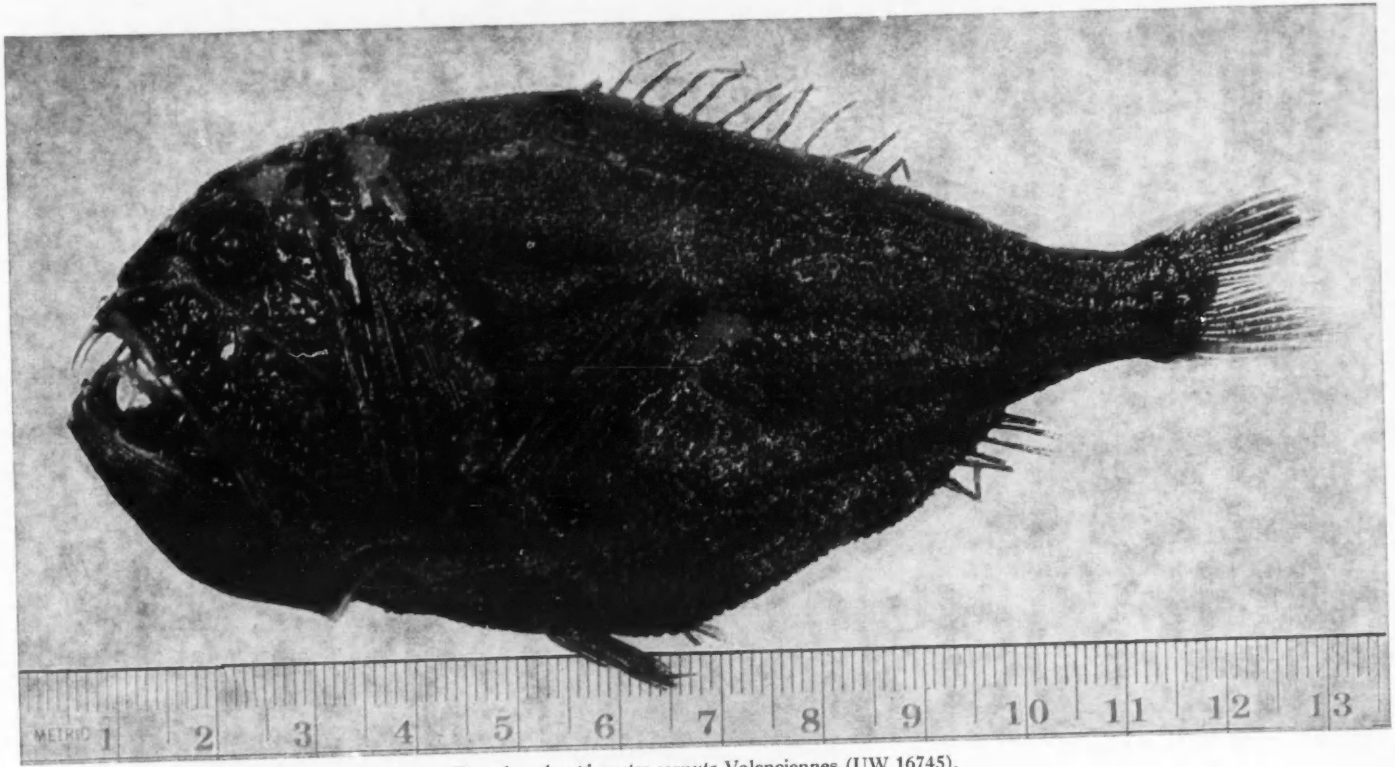
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FIG. 1. *Anoplogaster cornuta* Valenciennes (UW 16745).

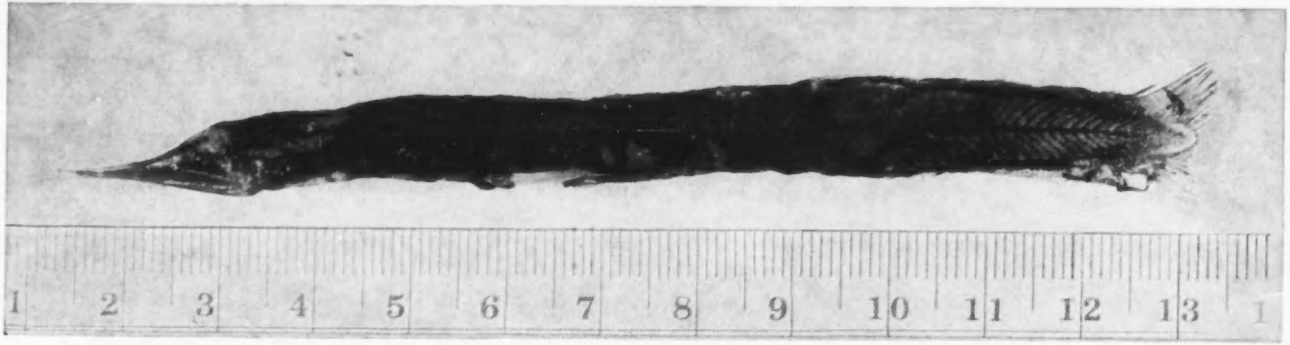
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FIG. 2. *Cyema atrum* Günther (UW 17549).

Grinols — J. Fish. Res. Bd. Canada

from the tip of the lower jaw for this specimen; the missing portion reduces the difference between L into Lt measurements from table VIII of Nybelin (1948), table III of Bertin (1937), and UW 17549. All circumorbital pores evident, except for one supraorbital pore on each side which was obscured by abraded epithelium. With the exception of the OD, OA, and possibly the OP interspaces the remaining taxonomic data do not show appreciable variation from previously recorded specimens (Bertin, 1937; Nybelin, 1948; Koefoed, 1955). Fresh and preserved specimen measurements (Lt, H, and P) indicate there was about an 11.5% loss in body form.

Distribution: *Cyema atrum* is a common, widespread species inhabiting all oceans at tropical to temperate latitudes (Grey, 1956). Ebeling (1962) gives the latitudinal distribution in the northeastern Pacific Ocean as ranging from off lower Baja California, Mexico, to off northern California (about in line with Cape Mendocino). The new record extends the known range of this species northward; the specimen was taken off Tillamook Head, Oregon, (45°45′N lat, 125°09′W long) from a 900-fath station, May 29, 1964.

Grey (1956) gives the maximum depth range recorded for adults at 437–2787 fath, the leptocephali larvae usually being found at more shallow depths.

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Exploratory Fishing and Gear Research Base
Seattle, Washington

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First Records of the Twoline Eelpout, *Bothrocara brunneum*, Greenland Halibut, *Reinhardtius hippoglossoides*, and Shortbelly Rockfish, *Sebastodes jordani*, in British Columbia Waters

Three species of fish, unrecorded for British Columbia waters, were collected in March 1965 from otter trawl catches of the Fisheries Research Board of Canada research vessel *G. B. Reed* off the west coast of Vancouver Island.

Bothrocara brunneum (Bean 1891) Twoline eelpout

On March 17, 1965, six specimens (340–562 mm, fork length) of the twoline eelpout, *Bothrocara brunneum* (Bean 1891), were collected off La Perouse Bank (48°44′N lat; 126°33′W long) in 301–318 fath (551–582 m) (haul no. GBR 65-2-47) (Fig. 1). Morphometric ratios and meristic counts fell within the ranges reported by Bayliff (MS, 1954).

A description and drawing of *B. brunneum* was given by Clemens and Wilby (1946) under the name of *B. mollis*. However, the specimen proved to be *B. molle* (Bayliff, 1959; Clemens and Wilby, 1961).

Bayliff (1954) reported the distribution of this species as from southern California to Kamchatka, but no specimens have been recorded from central Bering Sea to Washington.

The detailed description which follows is adapted to the format of Clemens and Wilby (1961).

Body very elongate, moderately slender, compressed. Head elongate, compressed, 4.5–5.2 in standard length; snout angular; eye, 5.2–6.5 in head on long axis; mouth terminal, slightly oblique; upper jaw overhanging lower; teeth small and numerous on jaw and palatine, on vomer 10–20; maxillary reaching to pupil, overhung by folds of skin; gill membranes joined far forward to isthmus so that gill opening extends well under head; gill rakers short and blunt. Fins: dorsal (1), 100–107, moderately high, confluent with caudal; anal, 89–95, confluent with caudal; dorsal and anal fins enveloped anteriorly in soft gelatinous tissue; pelvic absent; pectoral entire, about half length of head; caudal narrow, pointed. Lateral line: in two parts, upper beginning above pectoral fin base passing upward, parallel to back, ending just behind vertical from anus; lower commencing on mid-body above anus, passing above base of anal fin almost to posterior end of body, frequently becoming faint. Scales: cycloid, minute, covering body and vertical fins. Color: uniform light grey, semi-translucent; blue or black margin on dorsal and anal fins, color more intense posteriorly, transparent on narrow margins of vertical fins; light on lining of mouth; black on peritoneum.

Length to 26 inches.

Distinguished by two lateral lines; long axis of the eye shorter than the snout; gill rakers short and blunt, and the absence of pelvic fins.

Range: Southern California to western Bering Sea (Kamchatka).

The six specimens have been deposited in the museum of the Institute of Fisheries, University of British Columbia (Cat. No. BC 65-163).

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Reinhardtius hippoglossoides (Walbaum 1792) Greenland halibut

On March 13, 1965, a single specimen (mature female, 594 mm, fork length) of the Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), was caught (haul no. GBR 65-2-37) off La Perouse Bank (48°19′N lat; 126°06′W long) in 276–312 fath (505–561 m) (Fig. 2). Hubbs and Wilimovsky (1964) report the known geographical range in the Pacific Ocean as Japan to Baja California, but no specimens had been recorded from the Shumagin Islands to southern Oregon. This species also inhabits the arctic Atlantic Ocean (McAllister, 1960).

Morphometric ratios and meristic counts of the specimen fall within the ranges reported by Hubbs and Wilimovsky (1964). This species resembles the arrowtooth flounder (turbot), *Atheresthes stomias*, but is distinguished from it by a smaller eye; teeth uniserial, not barbed at tip; pores along the posterior edge of the preoperculum; and the angle of the preoperculum approximately 90° (Fig. 3).

The detailed description which follows is adapted to the format of Clemens and Wilby (1961).

> **Body rather elongate, slender, much compressed, dextral. Head elongate; mouth terminal, large, nearly symmetrical, gape wide; maxillary extending to point behind eye; teeth well developed on both jaws, uniserial; lower jaw projects; upper eye on margin of head. Fins: dorsal (1), 96; anal, 71; pelvic, 6; pectoral, 13. Lateral line: slightly curved, then straight, no arch or accessory branch. Scales: ctenoid, small, on both sides. No spines before anal fin. Color: black on eyed side, dark with light blotches on blind side.**
>
> **Length to 25 inches.**
>
> **Distinguished by the large projecting jaw; large, uniserial non-depressible teeth; black coloration on the blind side; and right angle posterior margin to the preopercular bone.**
>
> **Range: Baja California to Bering Sea (Japan, Atlantic).**

The specimen has been deposited in the museum of the Institute of Fisheries, University of British Columbia (Cat. No. BC 65-136).

Sebastodes jordani Gilbert 1895 Shortbelly rockfish

On March 14, 1965, 32 specimens of the shortbelly rockfish, *Sebastodes jordani*, were caught (haul no. GBR 65-2-40) off La Perouse Bank (48°22.7′N lat; 126°02′W long) in 100–110 fath (183–210 m) (Fig. 4). The size range of the specimens was 195–228 mm, fork length. There were 22 males and 11 females. All females carried eyed larvae.

Morphometric ratios and meristic counts were obtained from all specimens as per Phillips (1957), and the results compared with California specimens. British Columbia specimens had a smaller eye, shorter anal fin spines, and narrower caudal peduncle. No appreciable differences in meristic count ranges were noted. Following is a list of the three morphometric ratios, using head length as the numerator:

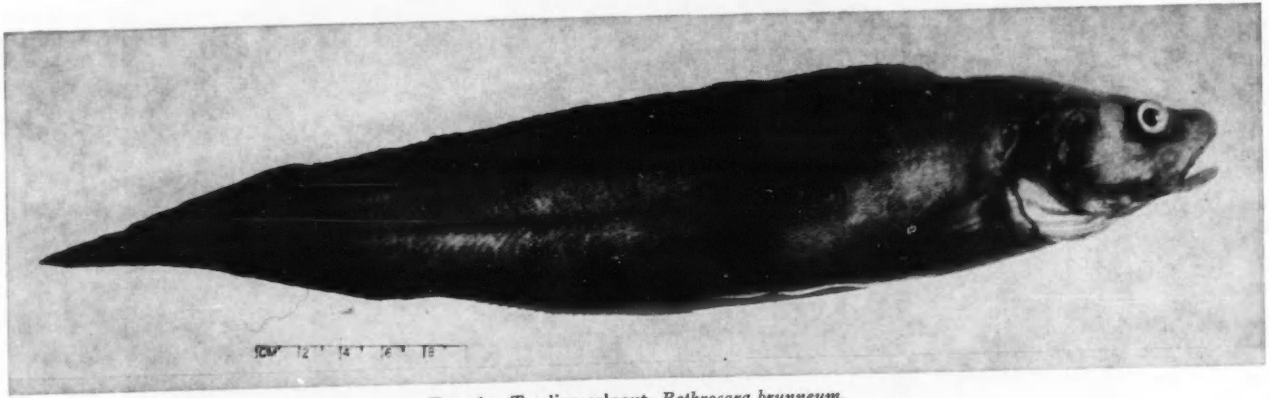
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FIG. 1. Twoline eelpout, *Bothrocara brunneum.*

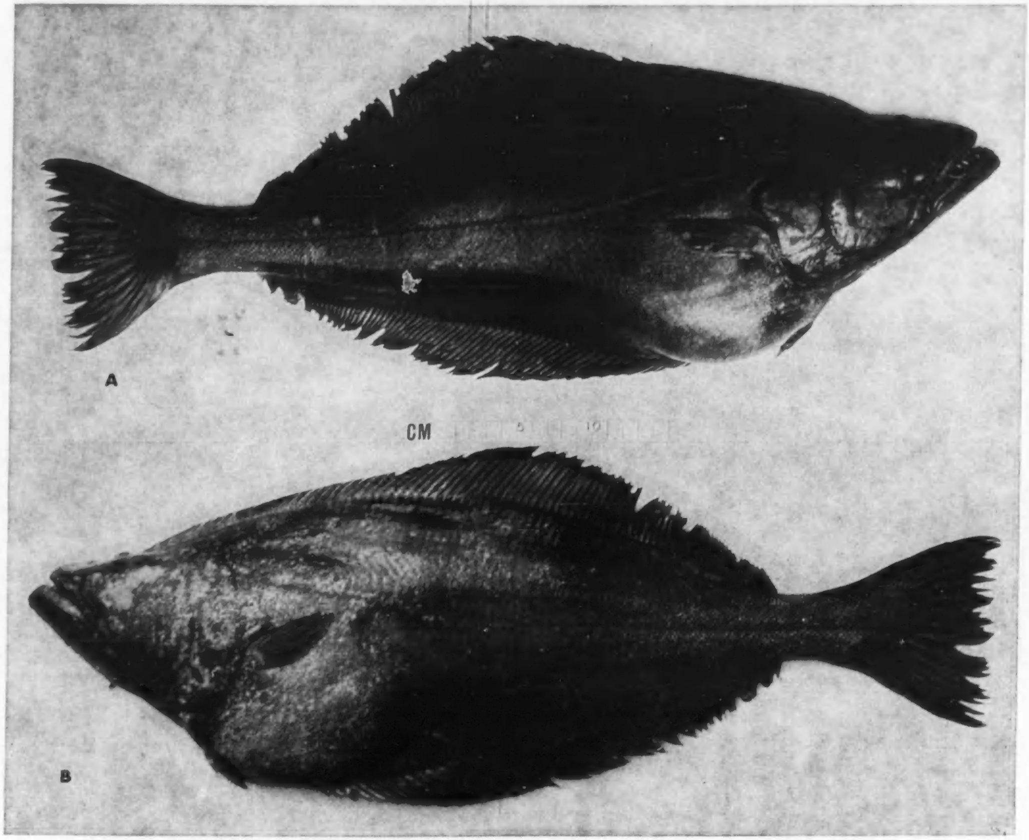

FIG. 2. Greenland halibut, *Reinhardtius hippoglossoides*. A — eyed side; B — blind side.

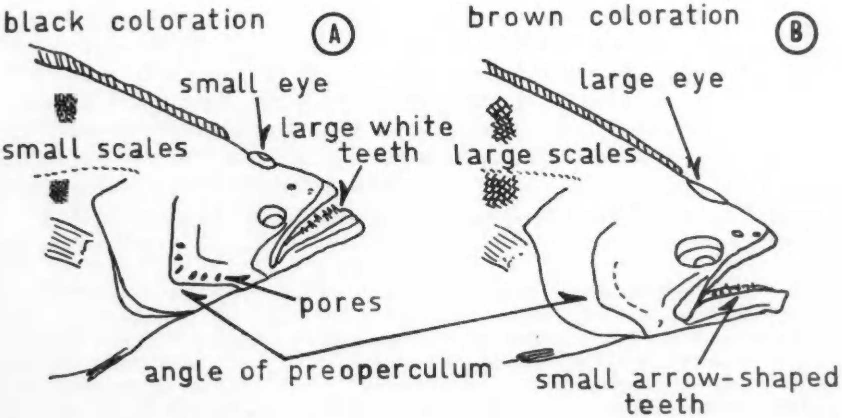
black coloration
A
small eye
large white teeth
small scales
pores
angle of preoperculum
brown coloration
B
large eye
large scales
small arrow-shaped teeth

FIG. 3. Characteristics used to differentiate (A) *Reinhardtius hippoglossoides* from (B) *Atheresthes stomias.*

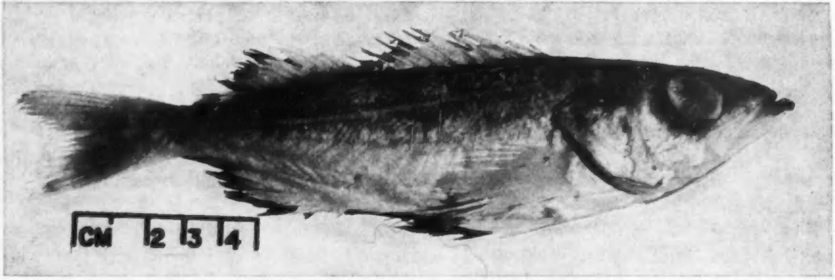

FIG. 4. Shortbelly rockfish, *Sebastodes jordani.*

Morphometric ratio	*California*	*British Columbia*
Orbit width into head length	3.8–4.0	3.1–3.9
Second anal fin spine into head length	3.1–3.4	3.7–5.2
Least depth caudal peduncle into head length	4.0–4.8	4.6–5.8

In a fresh or preserved condition, *S. jordani* resembles juvenile *S. paucispinis* in color and body shape, but can be distinguished from it by the location of the anus, midway between the origins of the ventral and anal fins. Also, the maxillary terminates beneath, or anterior to, the mid-orbit.

Phillips (1957) reported the geographic range as Ensenada, Baja California, to coast of Washington. Welander and Alverson (1954) reported the heretofore northernmost recaptures as 40 miles west of Lake Ozette, Washington (48°03′N lat), in 110 fath (201 m). The present record extends the known range of this species approximately 40 miles northward.

The detailed description which follows is adapted to the format of Clemens and Wilby (1961).

Body slender, depth 3.7–4.1 (3.8–4.1)[1] in standard length. Head moderate, upper profile slightly convex, 2.6–3.0 (2.9) in standard length; mouth terminal, moderate, lower jaw slightly projecting, upper jaw ending at or before mid-orbit; symphyseal knob small, sharp, forward-projecting; eye diameter 3.1–3.9 (3.8–4.0) in length of head; interorbital space at mid-orbits flat or slightly convex, broad, 4.3–5.1 (4.4–4.7) in head length; cranial spines weak; nasal and parietal always present; usually frontal III; rarely frontal II (adult fish); preopercular spines, small, sharp, lowermost one weak and occasionally absent; operculars 2, short, thin, sharp; lacrymal spines 2, anterior small and weak, posterior moderate and directed backward; rakers on first gill arch 41–46 (42–47). Fins: dorsal (1), XIII (XIV), 13–16 (XIII, (13) 14–15 (16)), deeply notched, membranes of spinous portion slightly incised; anal, III, 8–11 (III, (8) 9–10 (11)); pelvic, I, 5 (I, 5), thoracic, reaching anus; pectoral 19–21 (19–21), 12–15 (10–13) unbranched, reaching anus. Scales: ctenoid.[2] Pores: on lateral line 53–58 (52–59). Color: olive-pink dorsally becoming light pink. Fins: same color as adjacent body parts; peritoneum silver-grey with black dots or black.

Length to 12 inches.

Distinguished by slender body, maxillary extending to, or nearly to, mid-orbit, and anus midway between origins of anal and pelvic fins.

Range: Ensenada, Baja California, to southwest coast of Vancouver Island, British Columbia.

Sixteen specimens have been deposited in the museum of the Institute of Fisheries, University of British Columbia (Cat. No. BC 65-255), and a like number in the National Museum of Canada, Ottawa (Cat. No. NM65-131).

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[1] Numbers in parentheses are from Phillips (1957).

[2] Scale row counts unobtainable for the 32 specimens examined due to damaged squamation condition. Phillips (1957) reports 65–70 diagonal scale rows below lateral line for California specimens.

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Occurrences of the Fishes *Pholis schultzi* and *Liparis mucosus* in British Columbia

During field trips to the west coast of Vancouver Island by the Institute of Fisheries, several fishes rare to British Columbia were found. Of these, the pholid *Pholis schultzi* and the liparid *Liparis mucosus* have not been recorded from this province. In the following descriptions of British Columbian specimens, counts and measurements follow Hubbs and Lagler (1958) and are given as the mean followed by the range in parentheses. Collections are deposited in the Institute of Fisheries. Measurements are expressed as percentage of the standard length except where otherwise stated.

Pholis schultzi Hubbs in Schultz 1931 — Red gunnel

Spinous rays of dorsal fin, 85.4 (84–86). Anal: II, 42.1 (41–44); pectoral, 11.4 (11–12), pelvic, I, 1. Branched caudal rays, 12.8 (12–14). Body: width, 4.8 (3.5–5.4); depth, 9.6 (9.0–10.5). Head length, 11.7 (11.0–12.6). Eye diameter, 35.5 (28.7–38.7) of head length. Pre-anal length, 55.5 (53.3–57.6); predorsal length, 11.8 (11.3–13.0). Pectoral length, 35.5 (28.7–39.4) in length of head. Length of longest dorsal spine about 1.7–2.0. Length of longest anal ray about 2.8–3.3.

Body elongate, laterally compressed; greatest depth a little before anus. Eye small and placed high on head but not entering dorsal profile. Snout steep, its dorsal profile highly convex to occiput; in midline snout forms small rounded crest. Mouth: strongly oblique; maxillary reaching to below anterior margin of pupil; upper lip continuing as broad fold across snout; lower jaw with frenum. A short tubular nostril midway between median margin of upper lip and anterior margin of eye. Dorsal fin: base long; height short, shorter anteriorly; posterior membrane confluent with caudal fin. Anal fin: base long, origin closer to base of caudal fin than tip of snout; margin of membrane incised between rays; posterior end notched but confluent with caudal fin. Pelvic fins minute. Caudal fin rounded. Head pores, large; nasal pores, 2; suborbital pores, 5; postorbital pores, 6; occipital pores, 3; preopercular pores, 4; mandibular pores, 4.

Teeth strong, bluntly conical, slightly recurved; approximately in two rows on each jaw. Gill membranes united and free from isthmus. Four gill arches with small pore behind last one. About 13 gill rakers on first arch. Scales: cycloid, very small, embedded; covering body but absent on head.

Body usually bright dark red, but two specimens in collection BC 65-129 light brown and another specimen greenish-brown. Dorsal surface darker than ventral surface. Sides of body fairly plain or with variously developed serial patterns of light spots, blotches, or streaks that often blend into the lighter ventral surface. Series of about 16 small, evenly spaced, light markings along dorsal fin; anterior most light marking accentuated or obscured by black. Anal fin with a series of many dark and light vertical bars. Head with light bar passing ventrally from postero-ventral edge of eye and another bar passing ventrally from posterior portion of maxillary; both bars accentuated anteriorly and posteriorly with black bars; a few similar light bars may radiate from dorsal portion of eye; the more ventral light bars may be conspicuously white or filled in with some red or brown.

Rosenblatt (1964) compared all the species in the genus *Pholis*. In British Columbia *P. schultzi* can be distinguished from *P. laeta*, *P. ornata*, and *P. clemensi* by the presence of 84–86 dorsal spines and 41–44 soft anal rays. Two specimens of this species, 67 and 73 mm in standard length, were taken near Little Beach, Ucluelet, on December 13, 1964. Another two specimens, 63 and

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67 mm in length, were obtained near the same locality on March 5, 1965. Five more specimens between 52 and 74 mm in length were taken off a small island, between Long Beach and Schooner Cove, 7 miles south of Tofino, on March 6, 1965. These collections are catalogued respectively as BC 64-467, BC 65-128, and BC 65-129.

The areas from which these collections were taken are characterized by a rocky bottom, which is covered with pink calcareous algae and exposed to the surge of the waves from the open ocean. Collection BC 64-467 was taken during low tide and at depths down to 15 ft below the intertidal zone. Beyond this depth, the steep rocky shoreline graded into a bottom of shell or sand. Various red algae were abundant in a band 5–10 ft below the level of lowest tide and some large brown kelps were also scattered in the area. The other two collections were taken at similar depths below the intertidal zone but during a high tide of 11 ft. Collection BC 65-128 was from an area characterized by more large kelps and boulders. The locality of BC 65-129 was characterized by several patches of the eel grass *Zostera*.

Schultz and DeLacy (1936) record *Pholis schultzi* from California to as far north as the San Juan Islands, Washington. Therefore the specimens recorded here from near Tofino and Ucluelet represent the first record for British Columbia and the northern limit of the known range for *P. schultzi*. Hubbs (in Schultz, 1931) and Rosenblatt (1964) provide the only previously published descriptions of the species. These consist of diagnostic characters incorporated into taxonomic keys. Schultz and Hubbs (1961) discuss the confused introduction of the specific name into the scientific literature, provide the only illustration of the species, and designate a lectotype. Consequently, the above extensive description of nine British Columbia specimens is offered.

Liparis mucosus Ayres 1855 Slimy snailfish

Dorsal fin, 29.3 (28–30); anal, 23.1 (22–24); pectoral, 30.1 (27–32). Body depth, 23.6 (19.5–26.9); width, 18.0 (14.4–21.3). Distance from snout to origin of anal fin, 49.8 (44.4–55.0). Eye diameter, 17.5 (15.8–19.4) in length of head; diameter of disk, 52.7 (48.4–59.7) in length of head. Anus, 47.4 (40.0–52.7) in distance from disk to origin of anal fin.

Body elongate, stout anteriorly, compressed posteriorly; depth usually greater under first dorsal than over anal fin. Head depressed, broad. Mouth terminal; maxillary reaching to below a point half way between snout and eye. Teeth strongly trilobed, small. Snout bluntly rounded. Gill opening small, extending down to opposite bases of first three to six pectoral rays. Disk below gill opening. Skin loose, sometimes with broad low papillae. Minute, thin prickles often present. Dorsal fins: low; rays longer posteriorly, barely reaching to base of caudal fin; first dorsal low, rounded, shallowly notched posteriorly. Anal fin: low, reaching to base of caudal fin, posterior rays longer. Pectoral fin: rounded, placed immediately behind operculum, reaching to origin of second dorsal; lower rays slightly exserted, margin of membrane incised between lower rays. Caudal fin truncate to rounded.

One specimen in BC 62-881, two in BC 64-467, and three in BC 65-254 with horizontal-striped colour phase; specimens in first and last collection with broad, conspicuous, horizontal dark stripes over most of body but not on caudal fin, most of pectoral fin, or ventral surface of head or belly. Near dorsal surface the stripes are parallel to dorsal profile; on ventral surface they pass down from side of belly and are parallel to ventral profile of tail. The other two specimens mentioned above have much finer, less conspicuous stripes. Another specimen from BC 64-467,

bright uniform red, more pale on ventral surface. The striped specimens in BC 64-467 light yellowish between the stripes, but those of BC 65-254 more reddish or pink. Another specimen from BC 65-254 with an extensive polygonal or reticulated pattern on upper sides of head and body as well as on tail. Remaining specimens with a plain colour varying from brownish-pink, olive, brownish, to greenish-yellow. All specimens with thin dark bar at base of caudal fin and fine bars on caudal rays. Dorsal and anal fins tend to have more black pigment. Often a few small spots with light centres in series along lateral sides.

Liparis mucosus can be differentiated from the morphologically similar *L. florae* and *L. callyodon*, which are found in this same general area, by the fewer dorsal, anal, and pectoral rays; the gill slit extending down to between the bases of the third to sixth pectoral rays; and the low, rounded first dorsal fin. The margin of the membrane of the first dorsal fin does not fold back on itself when the fin is depressed as is the case with *L. florae*.

A specimen of *Liparis mucosus*, 46 mm in standard length, was taken by Dr Richard H. Rosenblatt and Mr Donald W. Wilkie at Agate Beach, 4 miles west of Sooke, on May 23, 1962. Another specimen, 30 mm in length, was taken at this locality on August 22, 1962. Although *Liparis mucosus* was not recognized in the revision by Burke (1930), Hubbs and Schultz (1934) provide a description and evidence for its recognition as a species. On December 13, 1964, and February 13, 1965, the Institute of Fisheries obtained 12 specimens near Little Beach, Ucluelet, Vancouver Island. These specimens from Agate Beach and Ucluelet are very similar to the description of Hubbs and Schultz (1934) and constitute the first records from British Columbia. The specimens from Ucluelet were found within the first 12 ft below the intertidal zone in an area exposed to the open ocean. The bottom was composed mostly of rock or boulders which were covered with pink calcareous algae and some red algae. The large kelps *Macrocystis* and *Nereocystis* were also dominant in the area. These collections of *Liparis mucosus* are catalogued as BC 62-871, BC 62-881, BC 64-467, and BC 65-254, respectively.

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